ECOLOGY AND POPULATION DYNAMICS OF PAMPA RODENTS NEAR BALCARCE, ARGENTINA

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ABSTRACT

ECOLOGY AND POPULATION DYNAMICS OF PAMPA RODENTS NEAR BALCARCE, ARGENTINA

By

Peter Lenn Dalby

A seventeen-month field study of the comparative ecology and population dynamics of three abundant grassland myomorphs was conducted on several one-hectare sites in the vicinity of Balcarce, Province of Buenos Aires, Argentina. These three species, namely, the herbivorous *Akodon azarae*, the granivorous *Oryzomys nigripes*, and the insectivorous *Oxymycteris rutilans* were compared with their "ecological equivalents", inhabiting temperate grasslands in North America. It was found that:

1. Populations of *A. azarae* during periods of high density exceeded 200 animals/hectare, comparable in density and rate of increase to that found in North American grass-eaters. By late winter the density was reduced to approximately 50 animals/hectare. Although sporadic population irruptions like those of North American *Sigmodon* and possibly *Oryzomys* occur, cyclic population fluctuations like those of microtines have not been reported. Typical of granivores, *O. nigripes* reached 50 animals/hectare the first summer and fall when the seed crop was abundant. By the following winter and early summer, the density was so reduced that several three-day trapping periods would pass before there were further captures. *Oxymycteris rutilans* had the lowest but most stable populations, with densities fluctuating between 3-15 mice/hectare.
2. Sex ratios of *A. azarae* suggested that, like in many other grass-

eaters, females make up a higher proportion of the total catch than males during the breeding (summer) season than in the non-breeding season. This was particularly true in resident versus recruit animals. *Oryzomys nigripes* consistently had a much smaller proportion of females, a feature common to the social organization of other seed-eaters. The proportion of female *O. rutilans* was higher, perhaps a function of its continual reproductive activity. Ratios of *A. azarae* coming into one of the study plots indicated that adult females dispersed less often than males during the breeding season, and about equally during the winter (non-breeding) season.

3. Reproduction of *A. azarae*, unlike other grass-eaters, from similar latitudes, was strongly seasonal, with litters born from the months of November to April. Litter size averaged 4.6, and gestation length, 22.7 days. Delayed implantation may occur. Young were successfully weaned at 14-15 days of age. The growth rate of the young did not attain the level found in the North American grass-eating microtines. Sexual maturity occurred at two months of age. Young born late in the year did not become sexually mature until the following breeding season. *Oryzomys nigripes* were noted to breed from January to May. Litter size averaged 3.6, but gestation period was not established. Young were successfully weaned at 14-15 days of age. Sexual maturity may not be reached until the following reproductive season. *Oxymycteris rutilans* bred in all seasons of the year. Litter size averaged 3.1, but gestation period was not established. Young were successfully weaned at 14 days of age. Sexual maturity occurred near three months of age. Although *A. azarae* is a seasonal breeder, the species realizes a much higher reproductive potential than the seed-eating *O. nigripes*

or the insect-eating *O. rutilans*. This agrees well with our knowledge of myomorph grass-, seed-, and invertebrate-eaters in North America.

4. The minimum survival rates for *A. azarae* averaged slightly higher during the winter (80-83 percent) than the summer (59-79.5 percent). Attrition during the winter season indicated that the survival rate was closer to 93-95 percent per fourteen days. *Oryzomys nigripes* had minimum survival rates near 60 percent for the time when they were most abundant. *O. rutilans* was calculated to have a survival rate of 70-76 percent during the summers, but in the winters it was closer to 92 percent. Dispersal, especially in summer, seemed to be a prime factor in lowering the minimum survival rates. Predation appeared to be insignificant. These findings make it difficult to establish whether *A. azarae*, *O. nigripes*, and *O. rutilans* have survival rates comparable to their North American ecological equivalents.
5. The spatial distribution (center of activity) of the mice on the study plots was influenced by vegetative cover. A shift in distribution for *A. azarae* and *O. nigripes* was noted in one plot when increasing numbers of guinea pigs (*Cavia aperea*) caused a deterioration in habitat quality. *Oryzomys nigripes* was captured rather homogeneously, but by the height of the habitat deterioration, had disappeared. On another plot where the vegetation consisted of a greater number of dominant grasses, *A. azarae* and *O. rutilans* were generally captured in the most heterogeneous habitat, whereas *O. nigripes* was found in the portion where vegetative cover was most dense and highest.
6. Movements (radii of activity) of *A. azarae* typified graminivorous rodents, being the least of the three species. Winter and male movements were only slightly longer than summer and female movements,

respectively. Female movements during a summer of high reproductive intensity were greatly restricted when compared to a summer when breeding was less intense. The vegetative destruction by *Cavia* seemed to be a factor favoring the increase in the radius of activity of *A. azarae* as the study progressed. Limited data for *O. nigripes* and *O. rutilans* showed only that their movements were 2-4 times more extensive than that for *A. azarae* and in general agreement with their North American counterparts. Dispersal information for *A. azarae* indicated that nearly 75 percent of the mice moved 100 m or less from their previous center of activity. This species homed readily considering the short distances tested (less than 200 m).

7. The diel activity patterns of *A. azarae* and *O. nigripes*, but not the insectivorous *O. rutilans*, agree with what is known of ecologically-similar species in North America. Specifically, the grass-eating *A. azarae* was active at nearly all times, with peaks during the crepuscular hours. The seed-eating *O. nigripes* was active exclusively at night. Unlike the nocturnal insectivorous North American grasshopper mice (*Onychomys*) which inhabit arid grasslands or the mesic-inhabiting shrew *Blarina brevicauda*, *O. rutilans* appeared to be exclusively diurnal. Energy demands and the type of food (grasses, grains, or insects) play a major role in dictating the activity pattern for each species. Although *A. azarae* is the primary myomorph herbivore, it appears to consume more invertebrates than North American grass-eaters. High metabolic rates for *A. azarae* are comparable to those of microtines. Burrowing and runway-making behaviors were less developed in *A. azarae* than the microtines. The above features indicate that the grass-eating *A. azarae* resembles

the North American grass-eating myomorphs in many respects. *Oryzomys nigripes*, in as much as the data will allow, typifies a long-tailed scansorial seed-eater, such as North American grassland forms of *Peromyscus* or *Reithrodontomys*. Only the insectivorous *O. rutilans* is a form not truly represented in North America and appears to have an ecological position overlapping those of both grasshopper mice, *Onychomys*, and shrews such as *Blarina*. The number of grass-eating and seed-eating myomorph species is comparable to that found at similar latitudes in tall grass areas of North America. A total of two myomorph grass-eaters (one uncommon), five seed-eaters (includes *Mus musculus*) and one insect-eater inhabited the study sites. The number of principal myomorph grass-eating species (one) to seed-eaters (four to five) agrees with the hypothesis suggesting that seed-eaters divide their consumer niche more efficiently than the grass-eaters. The seed-eaters of North American grasslands, unlike those found in this study, are augmented slightly in species numbers by the presence of the zapodids (jumping mice) and heteromyids (kangaroo rats, pocket mice). The insectivore niche may also allow several species to inhabit one area. *Oxymycteris rutilans*, and the marsupials, *Monodelphis dimidiata* and possibly *Lutreolina crassicaudata*, appear to fill the insectivore niche normally filled by *Onychomys* and shrews in North America.

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INTRODUCTION

While ecosystems are being examined more intently through computer models and field experimentation, demographic analyses of various organisms in the environment and studies of causal mechanisms to explain changes are necessities in applicable systems programs. Within several major biomes, a number of organisms, from different taxa and consumer levels are being studied. Likewise, similar biomes are being studied in different regions of the world to determine if the same ecological principles hold true. If not, then modeling and systems analyses are of limited use since their predictive values are diminished.

Grassland-inhabiting rodents are important components of pastoral ecosystems, not only economically, but also in their role as primary consumers. One method of studying ecological systems is through energetics, *i.e.*, according to each species consumer level. Baker (1971) discussed the nutritional aspects of grass-eating and seed-eating myomorphs found in North American grassland environs. These two groups have distinctive specializations as expressed by their morphological, physiological and behavioral characteristics. Ecologically, the two groups may be separated by certain distinctive features (Table 1).

The position of myomorph insect-eaters in such a table is uncertain. North American species are few (*e.g.*, both species of *Onychomys*). Hershkovitz (1962) believed that early myomorphs probably were forest dwellers, had low crowned and cuspidate teeth, and ate, in addition to insects and other invertebrates, seed, fruit, and other

Table I. Ecological parameters of myomorphs which differentiate temperate grass-eaters from seed- and insect-eaters. Best comparisons are made among sympatric species.

	GRASS-EATERS	SEED-EATERS
1.	Wide population fluctuations.	Narrow dramatic population fluctuations.
2.	Fast population turnover.	Slow population turnover.
3.	Temperature, nutrition primary factors regulating reproduction.	Photoperiod primary factor regulating reproduction.
4.	Early sexual maturity.	Late sexual maturity.
5.	No delayed implantation.	Delayed implantation if lactating.
6.	Short gestation periods.	Long gestation periods.
7.	Large litters.	Small litters.
8.	Many litters per reproductive season.	Few litters per reproductive season.
9.	Young partly precocious.	Young altricial.
10.	Diurnal or crepuscular activity pattern.	Nocturnal activity pattern.
11.	Hibernation or torpidity unknown.	Hibernation or torpidity common.
12.	Predators often diurnal or crepuscular.	Predators often nocturnal.
13.	Generally one species per area.	Generally two or more species per area.
14.	Small home ranges.	Large home ranges.
15.	Food selection restricted.	Food selection relatively broad.
16.	High annual biomass.	Low annual biomass, singularly or collectively.
17.	Much of total energy budget utilized in food gathering, assimilation.	Little total energy budget utilized in food gathering, assimilation.

plant products. Present-day seed-eaters and some grass-eaters continue to consume rather large quantities of animal food (Landry, 1970), especially during seasons when nutrient demands are greater (Fleharty and Olson, 1969). Since seed-eaters generally eat larger percentages of invertebrates than grass-eaters, it is best to place insectivorous species such as *Onychomys* with the former. The low densities of *Onychomys* as well as other characteristics (Bailey and Sperry, 1929; Horner *et al.*, 1964) also indicate that they are most similar to seed-eaters.

Compared to Nearctic grassland rodents, less is known about their counterparts in South America. Crespo (1966, 1970) and Pearson (1967) have been the main contributors to our knowledge of Argentine grassland rodent biology through snap-trapping techniques; Barlow (1969) has done likewise for adjacent Uruguay.

Purpose

This study summarizes an eighteen-month demographic analysis of a pampan myomorph rodent community on two study sites near Balcarce, Buenos Aires Province, Argentina. The principal myomorphs inhabiting these live-trapped sites included the field mouse, *Akodon azarae*, the peromyscine-like rice rat, *Oryzomys nigripes*, and the insectivorous burrowing mouse, *Oxymycteris rutilans*. Less common species were *Calomys laucha*, *C. musculinus*, *Cabreramys obscurus*, *Reithrodon auritus*, and *Mus musculus*. A hystricomorph, the guinea pig, *Cavia aperea*, and a small marsupial, *Monodelphis dimidiata*, also were present.

The objectives were two-fold: 1) to compare and contrast the demographic changes in a yearly cycle of rodent populations (the three principle species) inhabiting two different plant communities; and

2) compare these data, including pertinent ecological and behavioral observations, with that presently known about temperate grassland rodents in other parts of South America and especially North America.

Study Area

Biogeography

The Balcarce area, located approximately 37°45'S, 58°18'W, is part of a grassland steppe which covers all the province of Buenos Aires, parts of Santa Fe, Cordoba, La Pampa, and Entre Rios, and a large sector of Uruguay. Basically, this steppe is a transitional area, fundamentally and historically a subtropical faunistic retraction (since the Pliocene) with the addition and persistence of elements from the south and west (Ringuelet, 1960). Various workers, *e.g.* Cabrera and Yepes (1940), Ringuelet (1961) and Fittkau (1969), using mammals and other faunal elements, and Cabrera (1953, 1968) utilizing knowledge concerning general relief, soils, climate and vegetation, have attempted to delimit its boundaries. Figure 1 delimits a portion of the pampan steppe in the Province of Buenos Aires, as given by Ringuelet (1960) and Cabrera (1968), and denotes the location of Balcarce.

Physiography

The physiography (after Bourne, per. comm.; Borrello, 1968) of the Balcarce area, approximately 112 m above sea level, involves two distinct geological features. The first is the ancient (Precambrian and lower Paleozoic) mesa-like buttes or hills which constitute a part of the Sierras de Tandil and are scattered at irregular intervals. The second feature consists of the broad, level to gently rolling plains between such prominences.

The more rounded, somewhat lower hills are underlaid by granite

Figure 1. Buenos Aires Province, Argentina, showing its zoogeographic and phytogeographic divisions, and the location of Balcarce.

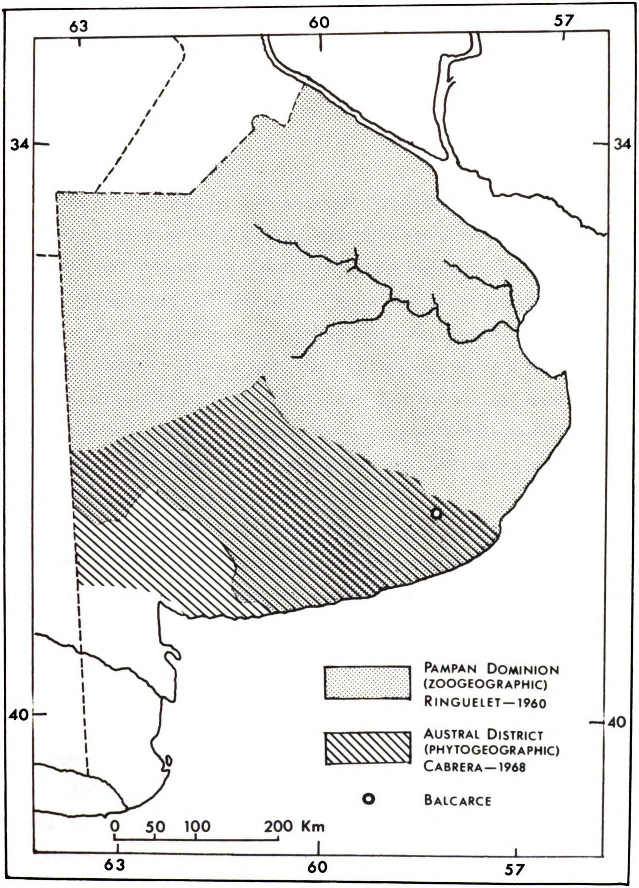

63
60
57
34
34
40
40
PAMPAN DOMINION (ZOOGEOGRAPHIC) RINGUELET—1960
AUSTRAL DISTRICT (PHYTOGEOGRAPHIC) CABRERA—1968
BALCARCE
0 50 100 200 Km
63
60
57

Figure I

which may be exposed. The more prominent mesas, composed mainly of quartzite, present abrupt slopes with steep colluvial slopes below, and are of little agricultural value. The plains themselves are a complex of either flat lowlands having poor external drainage, or slightly sloping to gently rolling uplands.

The soils in the area have developed from Quaternary sediments composed of water-worked loessal material with a high percentage of volcanic ash. Other than in the vicinity of the rock outcroppings and mesas, there are no soils developed from rock strata. In general, the soils of the well-drained uplands are of Brunizems. They have black (moist), granular, loamy, slightly acid surface soil with 4-8 percent organic matter. The subsoils, beginning at 15-40 cm, are clay loams with a strongly developed prismatic blocky structure. The substrata are loams to fine sandy loams. Lime hardpans and weakly consolidated loamy formulations begin at depths of 50-300 cm.

In the lowland areas with restricted drainage, the soils are dominantly solonetz and solodized solonetz with some solods in the better drained parts. These soils are characterized by very slowly permeable columnar or prismatic clay loam to clay subsoils with high sodium saturation and high pH.

Climate

The Balcarce climate is summarized in Table 2. Rainfall, which averages 836 mm annually, is most abundant in February and March, and least during the winter months (May-August). In the growing season, which runs for annual crops from about November through March, January is likely to be the driest month. Rain may be expected about every five or six days during any month of the year, with 75 percent of the rains

Table 2. The record of temperature, relative humidity, and rainfall at INTA, Balcarce (1941-1950).

Month	Mean Temp. °C	Mean Max. Temp. °C	Mean Min. Temp. °C	Absolute Min. Temp. °C	Relative Humidity %	Mean Precip. mm
January	20.3	28.9	13.3	3.8	63	46.5
February	20.1	28.0	13.7	5.6	69	86.9
March	17.1	23.9	11.7	2.5	74	112.8
April	14.4	20.5	9.2	-0.5	78	79.5
May	10.9	15.8	6.3	-2.4	82	55.1
June	8.4	13.0	4.3	-5.8	84	56.6
July	7.6	12.2	3.5	-4.0	83	61.7
August	8.1	13.5	3.6	-4.4	78	49.8
September	10.4	16.5	5.3	-3.4	75	73.7
October	13.7	20.5	7.4	-2.0	72	61.0
November	16.5	24.1	10.1	1.2	68	71.1
December	19.2	27.4	12.1	2.7	64	80.0
Yearly Basis	13.9	20.4	8.4	0.6	74	834.8 (Total)

being under 10 mm. Extended drought is rare.

Average monthly temperatures range from a low of 7.6°C in July to a high of 20.3°C in January. Nightly temperatures are frequently below freezing during winter months, but due to maritime influences, prolonged freezing temperatures and winter precipitation in the form of snow are very rare.

The relative humidity averages 74 percent for the year and ranges from 63 percent in January (summer) to 84 percent in June (winter) when evaporation and insolation are reduced. Wind velocity is generally moderate, varying around an average of 15 km/hr. The wind movement is greatest during December and January (summer) and least during May and June (winter).

During this study, increased rainfall (995.1 mm from January 1969 to December 1969) through all four seasons of the year was the most significant climatic change from the average.

METHODS

Study Plots and Trapping Schedules

The study plots were located on lands of the Experiment Station (INTA), approximately 15 km NW of Balcarce, and on the Augustín Crovetto property, situated about 6 km N of Balcarce.

Five of the six plots established to study the small mammal community were placed in Crovetto Pasture (Figure 2). This area, a 17 hectare lowland (100 m above sea level) fallow pasture with poor external drainage, was located adjacent to Highway 226 and a dirt road. A small creek, the Arroyo Pantanoso, bisected the pasture on its southernmost corner. Although seeded in 1965 with *Agropyron elongatum*, *Festuca arundinacea*, *Phalaris tuberosa*, *Lolium perenne* and *Trifolium pratense*, cattle grazing there for the next three years, up to and including the early part of the winter (June-July) of 1968 kept growth reduced. By the beginning of summer (November and December), the vegetational cover, although lacking ground litter, was well-developed, and a substantial rodent population quickly inhabited this unpastured land.

Because of the possibility, although remote, that part of the pasture might be grazed during the forthcoming year, the five study plots were established along the northwestern edge. Following is a description of them (Figures 3-8).

1. Plot I. Unenclosed, 1.2 hectares in area, a 10 x 10 trapping grid with 12 m spacing.

Three nights of live-trapping with Sherman live-traps scheduled every other week at 9-14 day (average, 14 days from middle of one trapping period to the middle of the next) intervals, depending on weather conditions. Basic demographic data described herein concerning the rodents in this pasture were gathered from this plot from December 1968 to April 1970.

2-3. Removal Plots I and II. Like Plot I in size but with each enclosed by an opaque plastic barrier (cleared for 50 cm on each side). The barrier, 40 cm high, 5 cm buried depth, 6 mil thickness was located 6 m from the nearest trap row of Plot I, and the perimeter trapping stations which they enclosed. Both Removal Plots were designed to test the effect of removal of the prominent mouse (Akodon azarae) on the population numbers of the remaining species. Live-trapping with removal of Akodon, but merely examining, marking, and releasing the other species was conducted for four consecutive days each month, from February 1969 (June for Plot II) to March 1970. Like the Activity Plot, data are given only in relation to dispersal movements.

4. Plot III. Enclosed, contiguous with Removal Plot I, a .13 hectares trapping grid of 3 x 3, with 12 m spacing, with perimeter trap stations 6 m from the exclosure. Instead of plastic, 50 x 120 cm interlocking tin sheeting, held upright by steel stakes, surrounded the plot. Because the guinea pig (*Cavia aperea*) increased in substantial numbers during the study and any dramatic change in small rodent population composition and structure which might have occurred in the Removal Plots was destroyed, Plot III was constructed in the spring (early December) of 1969 to determine what effect *Cavia* was having in depressing the local small rodent population by effectively excluding the former. Plans to replicate this experiment did not materialize when the remaining supply of sheeting became unavailable. The trapping schedule was four consecutive days each month from December 1969 to April 1970.
5. Activity Plot. Unenclosed, but contiguous with Plot I, .70 hectares in area, a 7 x 7 trapping grid, with 12 m spacing. This plot was live-trapped for three consecutive days every month (February 1969 to March 1970) with traps inspected at the end of every

three hour period, day and night. Data are utilized here only to describe general activity patterns for each of the three species.

6. Hill Plot. Like Plot I, unenclosed, 1.2 hectares in area, a 10 x 10 trapping grid, with 12 m spacing. Live-trapping initiated in March 1969 continued to April 1970, and followed the same schedule (generally trapped back-to-back or on the same days) as Plot I.

The latter study area, Hill Plot (Figures 9, 10, 11), was situated on a small hill within one km of INTA headquarters. The hill (5-10 percent overall slope, 150 m above sea level) was grazed or cultivated except for several hectares on the northeastern slope where rock outcroppings and thin soils predominated. This depauperate portion, on which Hill Plot was located, was undisturbed during INTA's 20 years of management. Cattle, preferring the surrounding areas of introduced pastures, only infrequently grazed on Hill Plot.

In contrast to the rather homogeneous vegetative cover and few major species found in the Crovetto Pasture, Hill Plot was quite heterogeneous, being covered by a correspondingly higher number of dominant plant species (Tables 3, 4). Dense patches of tall (1-2 m) _Paspalum quadrifarium_, a common grass of low areas and the slopes of the pampan sierras (Cabrera, 1953, 1968), covered about 40 percent of the area. The grasses _Piptochaetium montevidense_, _P. bicolor_, _Setaria geniculata_, and the pineapple-like (vegetatively, not reproductively) umbellifer, Eryngium paniculatum dominated the remainder.

Trapping Procedure and Data Recording

Sherman aluminum folding live-traps (75 x 75 x 227 mm), baited with rolled oats, were set within an hour or two of dusk and checked by early morning. After each 3-4 day trapping period, the traps were washed in a detergent-disinfectant solution, then rinsed and dried before further use. During the colder months, toilet paper was placed in the traps each night for nesting material. If the temperature was likely to approach freezing, additional external coverings, consisting of one or two cloths draped over each trap and then a 15 x 25 cm plywood sheet set on top, were applied in an effort to decrease trap mortality. Such efforts were especially necessary at the Crovetto Pasture where evening temperatures were nearly always lower than at the Hill Plot.

Traps containing animals were collected and brought to a tent shelter near each plot for processing. Individuals were toe-clipped, and weighed in a known-weight container placed on a 500 g Ohaus spring balance accurate to 1.0 g. The trap station, species, sex, individual number, weight, reproductive condition, and presence of external parasites (rodent bot flies, Cuterebridae) were recorded at every capture. Concerning reproductive condition, male mice were noted as scrotal or non-scrotal, females perforate or imperforate, and by abdominal palpation, pregnant or non-pregnant. Embryos were counted by palpation when they were of an easily detectable size. Age classes, consisting of juveniles, sub-adults, and adults, were designated, based when possible on the characteristics of known-age laboratory stock maintained for the study of comparative postnatal development.

Table 3. The common grasses and forbs of Plot I and Hill Plot. Those species marked with an * are characteristic of the Austral Pampan District, presented by Cabrera (1953, 1968).

PLOT I

Grasses
- Paspalum elongatum Griseb.
- P. vaginatum Siv.
- Festuca arundinacea Shreb.

Forbs
- Trifolium pratense L.
- Spilanthes stolonifera DC.
- Sida leprosa (Ort.) K. Sch.
- Phyla canescens (H.B.K.) Greene
- Ambrosia tenuifolia Spr.
- Cirsium vulgare (Savi) Airy-Shaw
- Solanum sp.
- Physalis sp.

HILL PLOT

Grasses
- *Paspalum quadrifarium Lam.
- *Piptochaetium montevidense (Spr.) Parodi
- *P. bicolor (Vahl.) Desv.
- *Stipa bonariensis Henr. et Parodi
- S. papposa Nees
- *Panicum bergii Arech.
- Setaria geniculata (Lam.) Beauvois
- Bouteloua sp.

Forbs
- Eryngium paniculatum Cav. et Dreeb.
- Oxalis montevidensis Prog.
- Senecio burchellii DC.
- Stevia multiaristata Spr.
- Chaptalia sp.
- Cirsium sp.
- Hyppochoeris sp.
- Zephyranthes sp.

Table 4. Percent cover found in Plot I and Hill Plot, summer 1969-1970.

PLOT I	
Grasses	
Agropyron elongatum	29.6
Festuca arundinacea	10.0
Forbs	
Phyla canescens	4.1
Cirsium vulgare	3.9
Sida leprosa	2.8
Others	
Misc. grasses and forbs	3.9
Litter	28.0
Bare ground	17.9

HILL PLOT	
Grasses	
Paspalum quadrifarium	44.5
Piptochaetium bicolor	12.4
P. montevidense	10.2
Setaria geniculata	1.1
Forbs	
Eryngium paniculatum	4.4
Chaptalia sp.	2.6
Cirsium sp.	1.2
Others	
Misc. grasses and forbs	4.1
Litter	14.5
Bare ground	5.0

General weather conditions and presence of predators were noted. Predator feces found on each plot during the trapping period were collected for later analyses. Mammalian nomenclature follows Cabrera (1961) except where more recent revisions pertain (Hershkovitz, 1959; Massoia and Fornes, 1967; Massoia *et al.*, 1968). Avian predators were identified according to Olrog (1959).

Vegetation Analysis

A 50 cm square wire frame was placed over undisturbed vegetation at a 50 cm distance from 30 randomly chosen trapping station stakes. An estimate of the percent vegetative cover in Plot I and Hill Plot was then made (Table 4).

An analysis of the Hill Plot cover during the summer of 1970 varied little in results from that taken in 1969. A partial analysis of Plot I during 1969 indicates that rather dramatic changes occurred between the summers of 1969 and 1970. Much of the change, resulting in an approximately 50 percent increase in ground litter cover and a 300 percent increase in bare ground, is directly attributable to an increase in density of the guinea pig, *Cavia aperea*, during this period. More about other qualitative and quantitative changes which occurred will be mentioned in a later section.

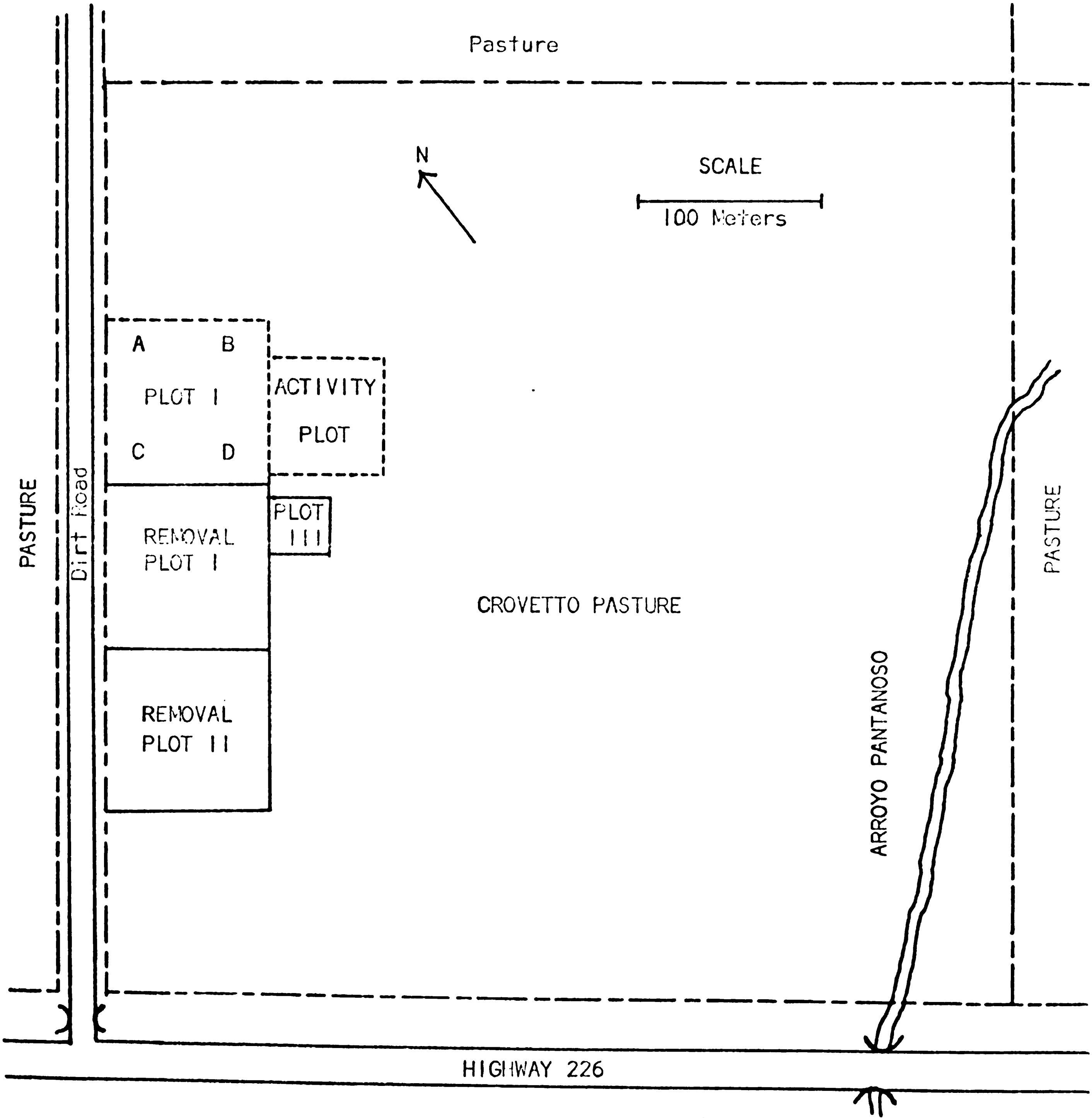


Figure 2. Crovetto Pasture, showing the approximate locations of the study plots. Plot I is divided into four quadrants.

Figure 3. Plot I mature growth of *Paspalum elongatum*, summer 1968-1969.

Figure 4. Removal Plot I (right) exclosure fence, taken near the back side of the Plot I, Removal Plot corner, summer 1968-1969. Major vegetation is *Paspalum elongatum*.

Figure 3

Figure 4

Figure 5. Plot I, winter 1969. Dominant vegetation is *Paspalum elongatum*.

Figure 6. Removal Plot I, winter 1969.

Figure 5

Figure 6

Figure 7. Plot I mature growth of *Paspalum elongatum*, summer 1969-1970. Note deterioration of dominant vegetation, and increase in forbs, particularly the thistle, *Cirsium*. Photo taken from the same approximate location as Figure 5.

Figure 8. Close-up taken from the approximate area shown in Figure 7. The cane debris covering the ground was produced by *Cavia*.

Figure 7

Figure 8

Figure 9. Diagramatic map of Hill Plot. Dots show pure stands of *Paspalum quadrifarium*, scattered pattern that of *Eryngium paniculatum*, and untouched areas, mixed stands of *Piptochaetium*, *Stipa*, and other grasses and forbs. The plot is divided into four quadrants, named A, B, C, and D, starting from the lower left-hand corner and going clockwise.

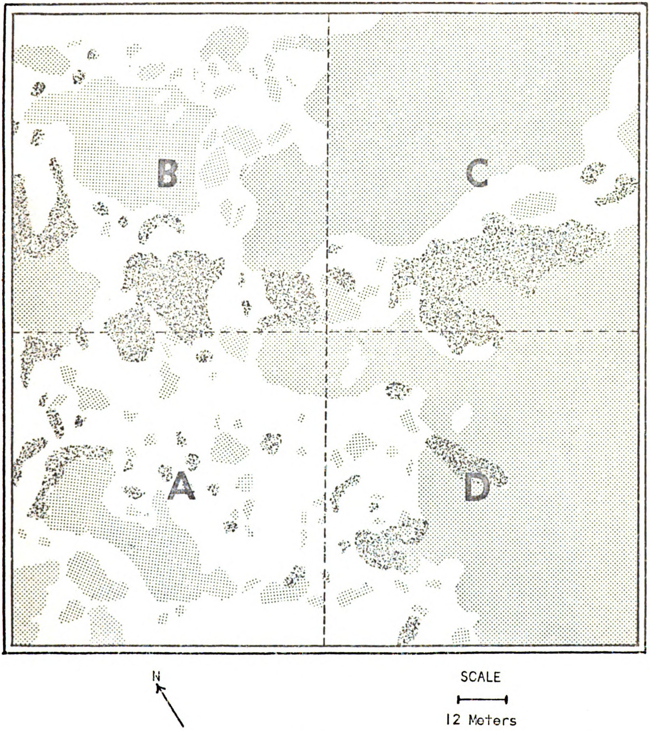


Figure 9

Figure 10. Hill Plot, summer 1969-1970, showing Paspalum quadrifarium to the left, Eryngium paniculatum mostly in the background, and Piptochaetium and Stipa, etc. in the foreground.

Figure 11. Hill Plot, summer 1969-1970, looking down the gentle slope. Piptochaetium, Stipa, etc. are in the foreground, Paspalum quadrifarium in the background. Several kilometers from this site and located on the farmland in the background is the Crovetto Pasture.

Figure 10

Figure 11

RESULTS

Population Density and Structure

Estimation of population densities

Random sampling was not attained either between the marked and unmarked segments of both populations or within the marked segment of each (see Leslie *et al*., 1953, and Krebs, 1966, for theoretical and practical discussions). The alternative method of population estimation, based on a rather intensive live-trapping program, is a direct enumeration, calculated by means of the Method B Grouping, given by Leslie *et al*. (1953).

The population estimates of *A. azarae* and *O. nigripes* (Figures 12, 13) throughout the study were highest in Plot I. The *O. rutilans*, however, maintained slightly higher numbers on Hill Plot. The *O. nigripes* population in Plot I, although it increased dramatically during late summer and early fall 1969, completely disappeared by the start of the following spring (after period 25), and never reappeared. Similarly, *A. azarae* never reached their previous year's level for equivalent periods in Plot I.

The percent deviation (Table 5) of the total catch for each trapping period from the minimum number known alive estimate is high, regardless of the species or season. No clear differences were observed due to these factors, however, and it is best just to summarize the data by noting that the minimum number generally ranged from 30-50 percent higher than the total catch.

Table 5. Percent deviation of the total catch (first column) from the minimum number known alive (middle column) for *Akodon azarae*, *Oryzomys nigripes*, and *Oxymycteris rutilans*. Calculated as $\left(\frac{\text{minimum number known alive}}{\text{total catch}}\right)100\% - 100\%$.

TRAP PERIOD	AKODON AZARAE						ORYZOMYS NIGRIPES			OXYMYCTERIS RUTILANS		
	PLOT I			HILL PLOT			PLOTS POOLED			PLOTS POOLED		
1 Dec. '68	43	43	0.0							2	2	0.0
2 " "	66	76	15.2				2	2	0.0	3	4	33.3
3 Jan. '69	119	131	10.1				5	5	0.0	3	5	66.7
4 " "	86	114	32.6					2		4	5	0.0
5 " "	81	109	34.6					2		4	6	20.0
6 Feb.	123	148	20.3				1	3	200.0	5	7	16.7
7 " "	118	168	42.4	52	52	0.0	1	7	600.0	1	7	600.0
8 Mar.	146	192	31.5	89	102	14.6	13	17	30.8	6	8	33.3
9 " "	129	199	54.3	83	121	45.8	34	40	17.6	6	10	66.7
10 Apr.	146	214	46.6	103	145	40.8	20	34	70.0	6	10	66.7
11 " "	127	187	47.2	103	145	40.8	33	51	54.5	8	12	50.0
12 May	111	185	66.7	116	153	31.9	63	74	17.5	7	13	85.7
13 " "	84	180*	114.3	101	143	41.6	46	64	39.1	7	12	71.4
14 June	111	179	61.3	114	142	24.6	22	54	145.5	6	13	116.7
15 " "	99	162	63.6	127	160	26.0	41	59	43.9	11	13	18.2
16 July	85	150	76.5	121	160	32.2	46	63	37.0	6	12	100.0
17 " "	93	146	57.0	112	141	25.9	53	59	11.3	8	14	75.0
18 " "	109	139	27.5	78	128	64.1	15	22	46.7	12	16	33.3
19 Aug.	107	143	33.6	100	129	29.0	17	20	17.6	15	17	13.3
20 " "	102	127	24.5	79	106	34.2	6	8	33.3	11	15	36.4
21 Sept.	61	83	36.1	63	90	42.9	3	5	66.7	14	17	21.4
22 " "	71	94	32.4	70	83	18.6	3	4	33.3	13	16	23.1
23 Oct.	81	99	22.2	74	80	8.1	4	5	25.0	15	16	6.7
24 " "	75	97	29.3	66	74	12.1	3	3	0.0	14	17	21.4
25 Nov.	78	93	19.2	36	42	16.7	2	2	0.0	6	14	133.3
26 " "	59	78	32.2	31	38	22.6	1	1	0.0	8	13	62.5
27 Dec.	57	69	21.1	14	23	64.3				7	12	71.4
28 " "	40	52	30.0	15	23	53.3				15	18	20.0
29 Jan '70	37	48	29.7	12	21	75.0				13	19	46.2
30 " "	30	47	56.7	17	25	47.1				9	18	100.0
31 " "	40	53	32.5	24	30	25.0				16	21	31.3
32 Feb.	35	55	57.1	28	33	17.9	3	3	0.0	17	22	29.4
33 " "	58	70	20.7	58	67	15.5	2	2	0.0	14	21	50.0
34 Mar.	92	104	13.0	71	97	36.6				13	19	46.2
35 " "	68	86	26.5	82	103	25.6	1	1	0.0	17	24	41.2
36 Apr.	77	77	0.0	86	86	0.0	4	4	0.0	16	16	0.0

* This percent deviation is probably related to a very heavy rainfall about a week subsequent to this period. Standing water remained in Plot I up to this date and several days more.

Trappability

The "trappability" (Krebs *et al.*, 1969) of the three species (Table 6) seems to vary with the season, plot and species involved. *Akodon azarae* was less trappable during high summer population levels and more trappable at low population levels in spring (during the Sept.-Dec. period when cover and food have been at a premium). Hill Plot *A. azarae* were slightly more trappable than those at Plot I, but whether this is a function of differences in density or other factors is unknown.

The diel activity patterns of the three species certainly affects the trappability of each. *Akodon azarae* activity is mainly crepuscular, that of *O. nigripes* strictly nocturnal, and that of *O. rutilans* diurnal (personal data). Since the traps were opened in the late afternoon, *A. azarae*, in accordance with their density, would enter the traps, thus excluding the other two species somewhat.

Limited quanities of *O. nigripes* preclude interpreting the trappability data, while data for *O. rutilans* suggest that they were most trappable on the Hill Plot. This perhaps was due to slightly lower *A. azarae* densities on the Hill Plot or the more dispersed pattern of habitation of *O. nigripes* on the latter plot, resulting in higher probabilities of finding an open trap.

Rate of increase

The rate of increase fluctuated considerably from one trapping period and plot to another for each species (Table 7). Part of this is due to differing trapping successes every period, while the major part reflects demographic changes in the populations. In *A. azarae*, the rate of increase lasted slightly longer at Hill Plot than Plot I in summer

Table 6. Trappability of *Akodon azarae*, *Oryzomys nigripes*, and *Oxymycteris rutilans*. Given is the total number (N) of animals captured, summed from the totals of six trapping periods, and the average percent catch of those known alive over that span.

	Akodon azarae				*Oryzomys nigripes*				*Oxymycteris rutilans*			
	Plot I		Hill Plot		Plot I		Hill Plot		Plot I		Hill Plot	
	N	Trap.	N	Trap.	N	Trap.	N	Trap.	N	Trap.	N	Trap.
Jan.-Mar. 1969	930	62.7			38	16.5	---	----	28	49.8	--	----
Apr.-June "	1107	56.3	888	69.0	235	37.0	101	66.0	24	12.5	49	79.3
July-Sept. "	788	67.5	754	70.8	130	85.3	47	43.2	39	48.2	52	80.3
Sept.-Dec. "	530	76.3	340	80.5	7	100.0	8	50.0	40	46.5	48	79.0
Jan.-Mar. 1970	325	65.7	199	56.7	0	-----	5	----	70	71.2	49	42.3

Table 7. Rate of increase for Akodon azarae, Oryzomys nigripes, and Oxymycteris rutilans, calculated as the percent change in population size from one trapping period to the next, based on the minimum number known alive.

	Akodon azarae				Oryzomys nigripes				Oxymycteris rutilans			
	Rate of Increase		Min. No. Alive		Rate of Increase		Min. No. Alive		Rate of Increase		Min. No. Alive	
	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot
1 Dec. '68			43				0				2	
2 " "	77		76		200		2		100		4	
3 Jan. '69	72		131		250		5		25		5	
4 " "	-13		114		-60		2		0		5	
5 " "	-4		109		0		2		20		6	
6 Feb. "	36		148		50		3		17		7	
7 " "	14		168	52	0		3	4	-43		4	3
8 Mar. "	14	96	192	102	33	225	4	13	-25	67	3	5
9 " "	4	19	199	121	500	23	24	16	0	40	3	7
10 Apr. "	8	20	214	145	-4	-31	23	11	0	0	3	7
11 " "	-13	0	187	145	48	55	34	17	33	14	4	8
12 May "	-1	6	185	153	56	24	53	21	25	0	5	8
13 " "	-3	-7	180	143	-13	-14	46	18	-20	0	4	8
14 June "	0	-1	179	142	-20	-6	37	17	0	13	4	9
15 " "	-10	13	162	160	14	0	42	17	0	0	4	9
16 July "	-7	0	150	160	10	0	46	17	0	-11	4	8
17 " "	-3	-12	146	141	0	-24	46	13	50	0	6	8
18 " "	-5	-9	139	128	-65	-54	16	6	17	13	7	9
19 Aug. "	3	1	143	129	-13	0	14	6	14	0	8	9
20 " "	-11	-18	127	106	-64	-50	5	3	-13	-11	7	8
21 Sept. "	-35	-15	83	90	-40	-33	3	2	0	25	7	10
22 " "	13	-8	94	83	-33	50	1	3	0	-10	7	9
23 Oct. "	5	-4	99	80	200	-33	3	2	0	0	7	9
24 " "	-2	-8	97	74	-33	-50	2	1	14	0	8	9
25 Nov. "	-4	-43	93	42	-50	0	1	1	-25	-11	6	8
26 " "	-16	-10	78	38	-100	0	0	1	-17	0	5	8
27 Dec. "	-12	-40	69	23	0	100	0	0	40	-38	7	5
28 " "	-25	0	52	23	0	0	0	0	71	20	12	6
29 Jan. '70	-8	-9	48	21	0	0	0	0	25	-33	15	4
30 " "	-2	19	47	25	0	0	0	0	-27	75	11	7
31 " "	13	20	53	30	0	0	0	0	9	22	12	9
32 Feb. "	4	10	55	33	0	300	0	3	0	11	12	10
33 " "	27	103	70	67	0	-33	0	2	-33	30	8	13
34 Mar. "	49	45	104	97	0	-100	0	0	-13	-8	7	12
35 " "	-17	6	86	103	0	100	0	1	14	33	8	16
36 Apr. "	-11	-17	77	86	0	300	0	4	-38	-31	5	11

1969. The summer 1970 increase in both populations apparently was not as large as that for the previous summer, indicated by the very slow and rather late increase (see especially Plot I) the second summer, followed by an earlier start of the population decrease.

Oryzomys nigripes, although in generally low numbers, shows the most varied rate, particularly in Plot I. On the other hand, O. rutilans remained the most stable of the three species. Consistent with their reproductive habits, discussed later, these animals showed no definite cycle of increases or decreases; rather, small increases and decreases could be expected at any time of the year. However, during the second summer both field populations experienced a short but definite period of increase, followed by a decrease to more or less the previous level.

Recruitment

Recruitment (Table 8) varied in each of the three species. The recruitment rate for A. azarae, based in percent (number of new animals recruited over the total individuals captured in each three day trapping period), remained high (Plot I, periods 2-10, 43.2 percent) until near the end of the first summer (breeding) season. With few exceptions, the winter (non-breeding) season recruitment was much lower and averaged for both plots, periods 11-24, only 13.5 percent, and did not reach its former high levels until the beginning of the second breeding season. At that time (periods 28-36), recruitment again climbed to its former levels, averaging 40.3 percent, plots pooled. Much of this jump can be attributed to Hill Plot, as Plot I alone averaged 28.8 percent, much lower than in the previous year.

Oryzomys nigripes and O. rutilans showed different trends than that found for A. azarae. The recruitment rate for O. nigripes

Table 8. Recruitment of new individuals of Akodon azarae, Oryzomys nigripes and Oxymycteris rutilans into Plot I and Hill Plot at each trapping period, as based on total captured each period.

	Akodon azarae						Oryzomys nigripes			Oxymycteris rutilans		
	Plot I			Hill Plot			Pooled Plots			Pooled Plots		
Trap period	Total Capt.	Recruits	Percent Recruits	Total Capt.	Recruits	Percent Recruits	Total Capt.	Recruits	Percent Recruits	Total Capt.	Recruits	Percent Recruits
1 Dec. 1968	43	(43)	100							2	(2)	100
2 " "	66	(45)	68				2	(2)	100	3	(3)	100
3 Jan. 1969	119	(77)	65				5	(5)	100	3	(1)	33
4 " "	86	(42)	49							5	(1)	20
5 " "	81	(25)	31							5	(3)	60
6 Feb. "	123	(66)	54				1	(1)	100	6	(3)	50
7 " "	118	(42)	36	52	(52)	100	1*	(0)	0	1*	(0)	0
8 Mar. "	146	(48)	33	89	(59)	66	13	(11)	85	6	(2)	33
9 " "	129	(27)	21	83	(41)	49	34	(29)	85	6	(2)	33
10 Apr. "	146	(47)	32	103	(39)	38	20	(16)	80	6	(1)	17
11 " "	127	(29)	23	103	(25)	24	33	(20)	61	8	(2)	25
12 May "	111	(12)	11	117	(27)	23	63	(34)	54	7	(2)	29
13 " "	84	(12)	14	101	(12)	12	46	(21)	46	7	(0)	0
14 June "	111	(9)	8	114	(11)	10	22	(6)	27	6	(1)	17
15 " "	99	(8)	8	127	(32)	25	41	(10)	24	11	(0)	0
16 July "	84	(7)	8	121	(23)	19	46	(16)	35	6	(0)	0
17 " "	92	(6)	7	112	(2)	2	53	(19)	36	8	(2)	25
18 " "	109	(7)	6	78	(1)	1	15	(5)	33	12	(2)	17
19 Aug. "	107	(15)	14	100	(12)	12	17	(8)	47	15	(2)	13
20 " "	102	(15)	15	79	(5)	6	6	(0)	0	11	(0)	0
21 Sept. "	61	(18)	30	63	(6)	10	3	(2)	67	14	(4)	29
22 " "	71	(21)	30	70	(4)	6	3	(1)	33	13	(2)	15
23 Oct. "	81	(14)	17	74	(7)	9	4	(2)	50	15	(1)	7
24 " "	75	(8)	11	66	(11)	17	3	(1)	33	14	(3)	21
25 Nov. "	78	(6)	8	36	(6)	17	2	(1)	50	6	(0)	0
26 " "	59	(3)	5	32	(7)	22	1	(1)	100	8	(0)	0
27 Dec. "	57	(5)	9	14	(1)	7				7	(3)	43
28 " "	40	(5)	13	15	(7)	47				15	(7)	47
29 Jan. 1970	37	(10)	27	12	(6)	50				13	(7)	54
30 " "	30	(9)	30	17	(8)	47				9	(3)	33
31 " "	40	(14)	35	24	(13)	54				16	(6)	38
32 Feb. "	35	(10)	29	28	(13)	46	3	(3)	100	17	(5)	29
33 " "	58	(23)	40	58	(44)	76	2	(2)	100	14	(5)	36
34 Mar. "	92	(45)	49	71	(45)	63				13	(3)	23
35 " "	68	(15)	22	82	(39)	48	1	(1)	100	17	(8)	47
36 Apr. "	77	(11)	14	86	(32)	37	4	(4)	100	16	(2)	13

*Corrected to account for first trapping period in Hill Plot.

Table 9. Recruitment of new individuals of Akodon azarae, Oryzomys nigripes and Oxymycteris rutilans into Plot I and Hill Plot at each trapping period as based on minimum number known alive.

Trap period	Akodon azarae						Oryzomys nigripes			Oxymycteris rutilans		
	Plot I			Hill Plot			Pooled Plots			Pooled Plots		
	Min. No. Capt.	Recruits	Percent Recruits	Min. No. Capt.	Recruits	Percent Recruits	Min. No. Capt.	Recruits	Percent Recruits	Min. No. Capt.	Recruits	Percent Recruits
1 Dec. 1968	43	(43)	100							2	(2)	100
2 " "	76	(45)	59				2	(2)	100	4	(3)	75
3 Jan. 1969	131	(77)	59				5	(5)	100	5	(1)	20
4 " "	114	(42)	37				2	(0)	0	5	(1)	20
5 " "	109	(25)	23				2	(0)	0	6	(3)	50
6 Feb. "	148	(66)	45				3	(1)	33	7	(3)	43
7 " "	168	(42)	25	52	(52)	100	7*	(0)	0	7*	(0)	0
8 Mar. "	192	(48)	25	102	(59)	58	17	(11)	65	8	(2)	25
9 " "	199	(27)	14	121	(41)	34	40	(29)	73	10	(2)	20
10 Apr. "	214	(47)	22	145	(39)	27	34	(16)	47	10	(1)	10
11 " "	187	(29)	16	145	(25)	17	51	(20)	39	12	(2)	17
12 May "	185	(12)	6	153	(27)	18	74	(34)	46	13	(2)	15
13 " "	180	(12)	7	143	(12)	8	64	(21)	33	12	(0)	0
14 June "	179	(9)	5	142	(11)	8	54	(6)	11	13	(1)	8
15 " "	162	(8)	5	160	(32)	20	59	(10)	17	13	(0)	0
16 July "	150	(7)	5	160	(23)	14	63	(16)	25	12	(0)	0
17 " "	146	(6)	4	141	(2)	1	59	(19)	32	14	(2)	14
18 " "	139	(7)	5	128	(1)	1	22	(5)	23	16	(2)	13
19 Aug. "	143	(15)	10	129	(12)	9	20	(8)	40	17	(2)	12
20 " "	127	(15)	12	106	(5)	5	8	(0)	0	15	(0)	0
21 Sept. "	83	(18)	22	90	(6)	7	5	(2)	40	17	(4)	24
22 " "	94	(21)	22	83	(4)	5	4	(1)	25	16	(2)	13
23 Oct. "	99	(14)	14	80	(7)	9	5	(2)	40	16	(1)	6
24 " "	97	(8)	8	74	(11)	15	3	(1)	33	17	(3)	18
25 Nov. "	93	(6)	6	42	(6)	14	2	(1)	50	14	(0)	0
26 " "	78	(3)	4	38	(7)	18	1	(1)	100	13	(0)	0
27 Dec. "	69	(5)	7	23	(1)	4				12	(3)	25
28 " "	52	(5)	10	23	(7)	30				18	(7)	39
29 Jan. 1970	48	(10)	21	21	(6)	29				19	(7)	37
30 " "	47	(9)	19	25	(8)	32				18	(3)	17
31 " "	53	(14)	26	30	(13)	43				21	(6)	29
32 Feb. "	55	(10)	18	33	(13)	39	3	(3)	100	22	(5)	23
33 " "	70	(23)	33	67	(44)	66	2	(2)	100	21	(5)	24
34 Mar. "	104	(45)	43	97	(45)	46				19	(3)	16
35 " "	86	(15)	17	103	(39)	38	1	(1)	100	24	(8)	47
36 Apr. "	77	(11)	14	86	(32)	37	4	(4)	100	16	(2)	13

*Corrected to account for first trapping period in Hill Plot.

remained very high at all seasons, averaging 61.0 percent for periods 1-36, plots pooled (data corrected to account for first trapping period of each plot). The *O. rutilans* data, examined in the same manner, presented a more stable condition than the former species, averaging 25.9 percent. Although reproduction was found to occur in this species throughout the year, there was a high recruitment for the two summer seasons (average, 38.4, 30.3 percent, respectively) and less than half this during the winter season (average, 14.1 percent).

If the recruitment rate is based on the minimum number of known alive instead of the total individuals captured, the results, although essentially the same, show lower and less variable rates (Table 9). Then recruitment for *A. azarae* for the first breeding season dropped from 43.2 to 34.3 percent; for the non-breeding season, both plots pooled, formerly 13.5, now 9.9 percent, and for the second breeding season, from 40.3 to 31.2 percent. Hill Plot, as before, contributed to much of the latter since Plot I averaged only 22.3 percent.

Recruitment rates for *O. nigripes* now averaged 47.3 instead of 61.0 percent for periods 1-36, plots pooled. For *O. rutilans* during the same period, recruitment dropped from 25.9 to 21.5 percent. The two summer seasons were now 29.2 and 27.2 instead of 38.4 and 30.3 percent, respectively, and the winter season rate dropped to 10.0 from 14.1 percent.

Sex ratios

Sex ratios of *A. azarae* born in captivity do not deviate statistically from the expected 1:1 (Appendix A). Laboratory neonate data for *O. nigripes* and *O. rutilans* were meager, since few were sexed at birth, and later death precluded obtaining these data. This section examines, through several methods, the changes in sex ratios which occur under field conditions. Field data were first tabulated for the three species to determine the percentage of females found in each trapping period (Table 10).

Sex ratios in *A. azarae* favor a higher proportion of females during the breeding season, although not necessarily over .500. During the first breeding season (periods 1-10) in Plot I, an average 54.6 percent of the mice were females. During the second breeding season (periods 25-34), the percentages were 48.9 and 51.6 percent, respectively, for Plot I and Hill Plot. In contrast, the non-breeding season (periods 11-24) percentages averaged lower for the two plots, 45.6 and 43.1 percent, respectively. Sex ratio data (pooled plots) for *O. nigripes* and *O. rutilans* showed that female *O. nigripes* were consistently below 50.0 percent (average, 28.4) while female *O. rutilans* averaged higher, or 59.2 percent.

Goodness of fit X^2 analyses, according to age class, season, and status (resident or recruit), were also completed for *A. azarae* (Table 11). Since this species was snap-trapped in reasonable numbers in other areas of Crovetto Pasture, these data also are included. Either because of small sample sizes, and/or the non-seasonality of reproduction, similar data (Table 12) for *O. nigripes* and *O. rutilans* are less complete.

The status of an individual was determined as defined by Meyers and Krebs (1971). Specifically, resident mice were those captured during any one three-day trapping period. Originally, however, they had been first captured in a previous trapping period. These mice, then, have been plot residents for a minimum of 9-14 days, the normal time

Table 10. Proportion of female *Akodon azarae*, *Oryzomys nigripes* and *Oxymycteris rutilans* captured in each trapping period.

Trap Period	*A. azarae*		*O. nigripes*	*O. rutilans*
	Plot I	Hill Plot	Plots Pooled	
1 Dec. 1968	.512	-	-	.000
2 " "	.606	-	.500	.667
3 Jan. 1969	.664	-	.333	.667
4 " "	.686	-	-	.600
5 " "	.519	-	-	.800
6 Feb. "	.512	-	.000	.333
7 " "	.441	.250	.400	.500
8 Mar. "	.500	.348	.154	.500
9 " "	.488	.325	.265	.667
10 Apr. "	.534	.456	.400	.667
11 " "	.417**	.476**	.242	.625
12 May "	.451**	.393**	.349	.571
13 " "	.464**	.456**	.370	.714
14 June "	.496**	.447**	.409	.667
15 " "	.495**	.433**	.463	.727
16 July "	.471**	.438**	.413	.667
17 " "	.452**	.384**	.453	.625
18 " "	.459**	.372**	.267	.583
19 Aug. "	.505**	.420**	.412	.667
20 " "	.510**	.405**	.500	.636
21 Sept. "	.410**	.444**	.000	.571
22 " "	.380**	.471**	.333	.615
23 Oct. "	.444**	.446**	.500	.533
24 " "	.427**	.455**	.000	.643
25 Nov. "	.513	.360	.000	.500
26 " "	.407	.406	.000	.625
27 Dec. "	.421	.571	-	.857
28 " "	.500	.533	-	.733
29 Jan. 1970	.460	.667	-	.462
30 " "	.533	.765	-	.444
31 " "	.550	.542	-	.563
32 Feb. "	.457	.601	.667	.588
33 " "	.552	.362	.000	.714
34 Mar. "	.500	.352	-	.538
35 " "	.441**	.427**	.000	.471
36 Apr. "	.494**	.430**	.250	.563

**Indicates non-breeding season for *A. azarae*.

Table II. Proportion of female A. azarae of various age and status (recruits, residents) classes, and seasons found in Crovetto Pasture and Hill Plot. Female sample sizes (in parentheses) and probabilities for null hypotheses of 1:1 sex ratios are also given.

	JUVENILES			SUBADULTS			
	First Breeding Season	Second Breeding Season	Breeding Seasons Pooled	First Breeding Season	Second Breeding Season	Breeding Seasons Pooled	Non-Breeding Season
Plot I All Capt.	.635 (40) .05>p>.025	.400 (6) p>.10	.590 (46) p>.10	.570 (130) .05>p>.025	.588 (30) p>.10	.573 (160) .025>p>.01	.736 (39) p<.005
Plot I Recruits	.638 (30) .10>p>.05	.417 (5) p>.50	.593 (35) p>.10	.591 (91) .025>p>.01	.595 (25) p>.10	.592 (116) .025>p>.01	.684 (13) p>.10
Crovetto Pasture (snap-trap)	---	---	.438 (7) p>.50	---	---	.365 (19) .10>p>.05	.667 (38) .025>p>.01
Hill Plot All Capt.	---	.462* (12) p>.50	.462 (12) p>.50	---	.422 (19) p>.10	.422 (19) p>.10	.700 (69) p<.005
Hill Plot Recruits	---	.462 (12) p>.50	.462 (12) p>.50	---	.419 (18) p>.10	.419 (18) p>.10	.783 (36) p<.005
Hill Plot Residents	---	---	---	---	---	---	.623 (33) .10>p>.05
Plot I Residents	.677 (6) p>.10	.333 (1) p>.50	.583 (7) p>.50	.543 (38) p>.10	.556 (5) p>.50	.544 (43) p>.10	.765 (26) p<.005

*Includes animals from last part of previous breeding season.

Table II (Continued).

	ADULTS				ALL AGES			
	First Breeding Season	Second Breeding Season	Breeding Seasons Pooled	Non-Breeding Season	First Breeding Season	Second Breeding Season	Breeding Seasons Pooled	Non-Breeding Season
Plot I All Capt.	.523 (401) p>.10	.485 (223) p>.50	.509 (624) p>.50	.447 (564) p<.005	.540 (571) .01>p>.005	.492 (259) p>.50	.524 (830) .10>p>.05	.459** (604) p<.005
Plot I Recruits	.463 (113) p>.10	.382 (29) .05>p>.025	.444 (142) .05>p>.025	.484 (78) p>.50	.526 (234) p>.10	.454 (59) p>.10	.510 (293) p>.50	.506 (91) p>.50
Crovetto Pasture (snap-trap)	.466 (34) p>.50	.514 (18) p>.50	.481 (52) p>.90	.454 (88) p>.10	.460 (57) p>.10	.500 (21) p=1.00	.470 (78) p>.10	.502 (126) p>.90
Hill Plot All Capt.	---	.460 (114) p>.10	.460 (114) p>.10	.410 (500) p<.005	---	.456 (139) p>.10	.456 (139) p>.10	.431 (569) p<.005
Hill Plot Recruits	---	.383 (36) .05>p>.025	.383 (36) .05>p>.025	.442 (57) p>.10	---	.399 (59) .025>p>.01	.399 (59) .025>p>.01	.531 (93) p>.10
Hill Plot Residents	---	.506 (78) p>.50	.506 (78) p>.50	.406 (443) p<.005	---	.506 (78) p>.50	.506 (78) p>.50	.389 (407) p<.005
Plot I Residents	.553* (271) .025>p>.01	.505 (194) p>.50	.532 (465) .10>p>.05	.441 (486) p<.005	.554 (315) .025>p>.01	.505 (200) p>.50	.534 (515) .05>p>.025	.451 (512) p<.005

* First weeks catch not included since no chance of previous capture.

**Includes one juvenile.

between the end of one trapping period and the start of another. Recruits were those captured on the grid for the first time during any one of the three-day trapping periods. Meyers and Krebs have stated that resident sex ratios are indicative of the effective sex ratio of a more or less stable "resident" population, while recruits give an estimate of the potential on which selection can act to arrive at resident sex ratios.

On examination of Table II, juvenile _A. azarae_ did not differ significantly from the expected 1:1 sex ratio except at one period. Subadults were somewhat mixed in sex ratios with significant trends ($p < .05$) strongest during the non-breeding season, where a high proportion of females were favored. Very likely a major contributing factor for this phenomenon is the fact that adult female weights average less than males, resulting in a greater number of females falling into the subadult class. This is reflected in the adult class where suddenly the proportion of females during the non-breeding season was less than .500 in all cases. Other than with non-breeding season adults, in all but two cases breeding season females were not significantly different from the expected 1:1 sex ratio. When all ages are pooled, the results, as before, suggest that females during the breeding season constitute a larger part of the trappable population than during the non-breeding season. This trend was especially influenced by resident rather than recruited animals.

The generalizations mentioned above for _A. azarae_ hold true for both study sites, with the exception of the snap-trap results. When differences did occur of a rather large magnitude, it could be attributed to small sample sizes (_e.g._, Plot I subadult all captures, first breeding season effect on pooled breeding season results).

The significance of the snap-trap, live-trap disparity should be examined more closely in the future. Yang et al. (1970) found no differances between sexes when Museum Special snap-traps were tested against Longsworth (prebaited) live-trapping of Indiana Microtus populations.

Plot I and Hill Plot sex ratio data were pooled for O. nigripes and O. rutilans to increase the sample size and then analyzed (Table 12). The results indicate that there were no significant differences in the expected 1:1 sex ratio of the juvenile-subadult groups. However, the proportion of adult female O. nigripes was significantly lower than expected, and this result held even when all age classes were pooled. The same type of analysis for adult females of O. rutilans showed just the opposite since adult females represented a significantly higher proportion of the trappable population than expected. When sex ratios of recruits were compared to those of residents in the same table, O. nigripes residents and recruits both showed significantly fewer females than expected. On the other hand, O. rutilans recruits did not differ significantly from the expected 1:1 ratio, but the residents did.

Reproduction

Although seasonal reproductive changes in a mouse population are best analyzed by an intensive snap-trapping and autopsy program, it also necessitates sacrificing animals from the community under study or at least from an area in close proximity.

The reproductive field data presented here, therefore, are based on finger palpation (Godfrey, 1953; Ranson, 1941) of sexually mature females. This technique is criticized for being inaccurate, and possibly traumatic to both the embryos and the female. With practice, however, palpation can be considered very reliable, except when a large number of embryos may

Table 12. Sex ratio data on *Oryzomys nigripes* and *Oxymycteris rutilans*, Plot I and Hill Plot pooled, shown with proportion of females, sample sizes (in parentheses), and lastly, probability for null hypotheses of 1:1 sex ratios.

	Oxymycteris rutilans		*Oryzomys nigripes*	
	Juv. + SA pooled	Age classes pooled	Juv. + SA pooled	Age classes pooled
All captures (plots pooled)	.605 (26) $p > .10$	.593 (200) $p < .005$	.444 (4) $p > .10$	.366 (164) $p < .005$
Recruits (plots pooled)	----	.547 (47) $p > .10$	----	.353 (78) $p < .005$
Residents (plots pooled)	----	.614 (151) $p < .005$	----	.381 (85) $p < .005$

make accurate counting difficult. If the embryos are small and easily discernible from each other, palpation appears to have little effect on the development of the embryos or the health of the female.

What is known about the reproductive biology of _A. azarae_, _O. nigripes_, and _O. rutilans_ has been gathered to date through snap-trapping studies (Crespo, 1966, 1970; Barlow, 1969). More information, gathered under laboratory and field conditions, is necessary to fully understand the reproductive patterns of these species. Since little has been previously published on reproductive periods, litter sizes, postnatal development, etc., these data are presented in Appendix A.

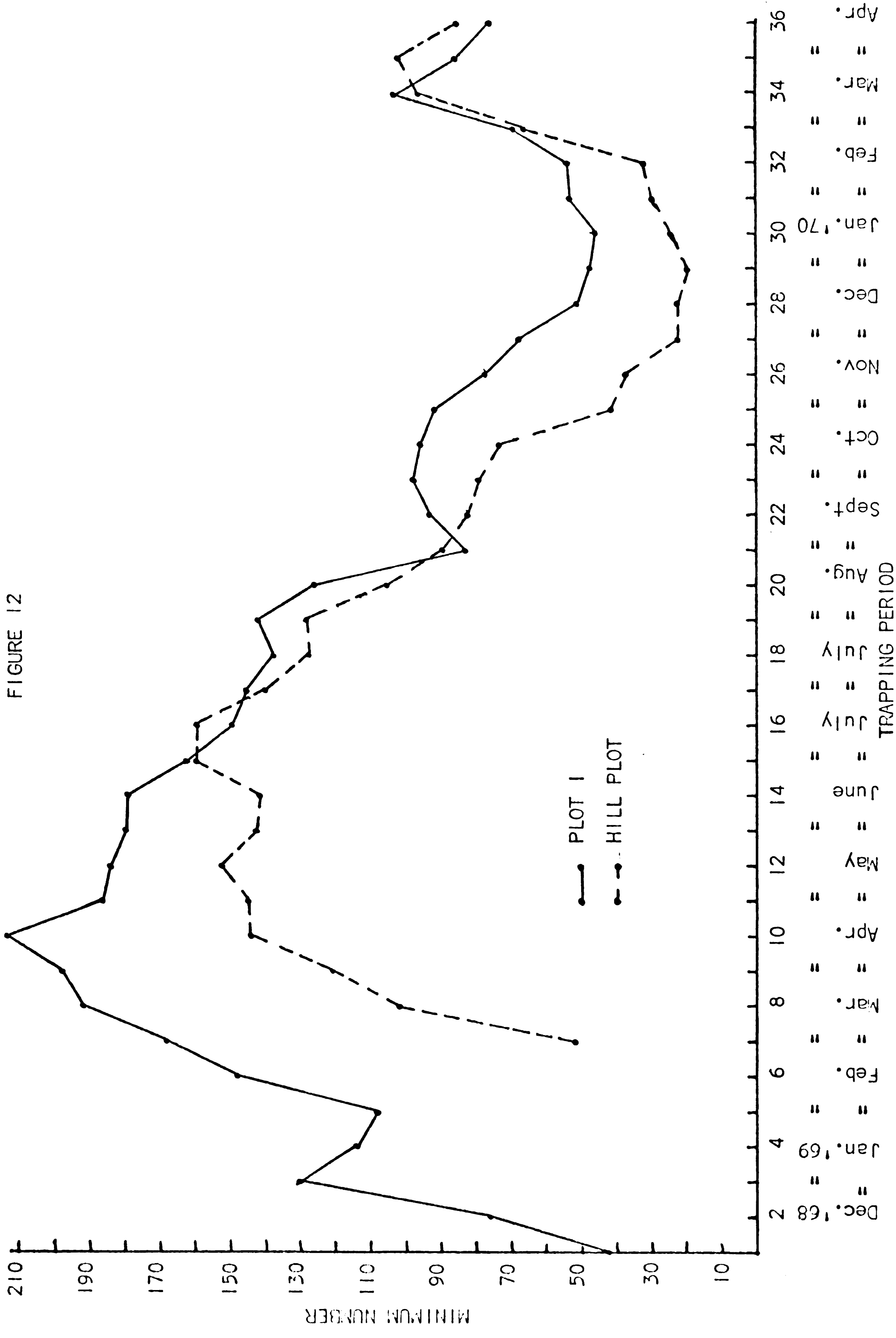
Weight of reproductive animals

In order to express reproductive activity as a function of weight, it is imperative to remember several points. First, if old animals are the sole members of the trappable population during spring and early summer, they will tend to make weight minimums high. Second, weights of reproductive animals midway in the season may be low because of the large proportion of young individuals. Third, young born late in the reproductive season will attain the weights commonly found for reproductive animals, but may not develop sexually until the following season.

The average weight of reproductive animals for each trapping period was established by summing the weights of all animals showing a particular sexual trait (e.g., scrotal testes). Depending on the type of analyses involved, a number of periods were grouped to give average weights. By doing so, it was possible for an animal to be recorded more than once, although the population's average weight should not be far from that expected if one sampled from the middle of the grouped

Figure 12. Minimum number estimates of _Akodon azarae_ in Plot I and Hill Plot.

FIGURE 12


PLOT I
HILL PLOT
MINIMUM NUMBER
210
190
170
150
130
110
90
70
50
30
10
TRAPPING PERIOD
2
4
6
8
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12
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16
18
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24
26
28
30
32
34
36
Dec.'68
Jan.'69
Feb.
Mar.
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May
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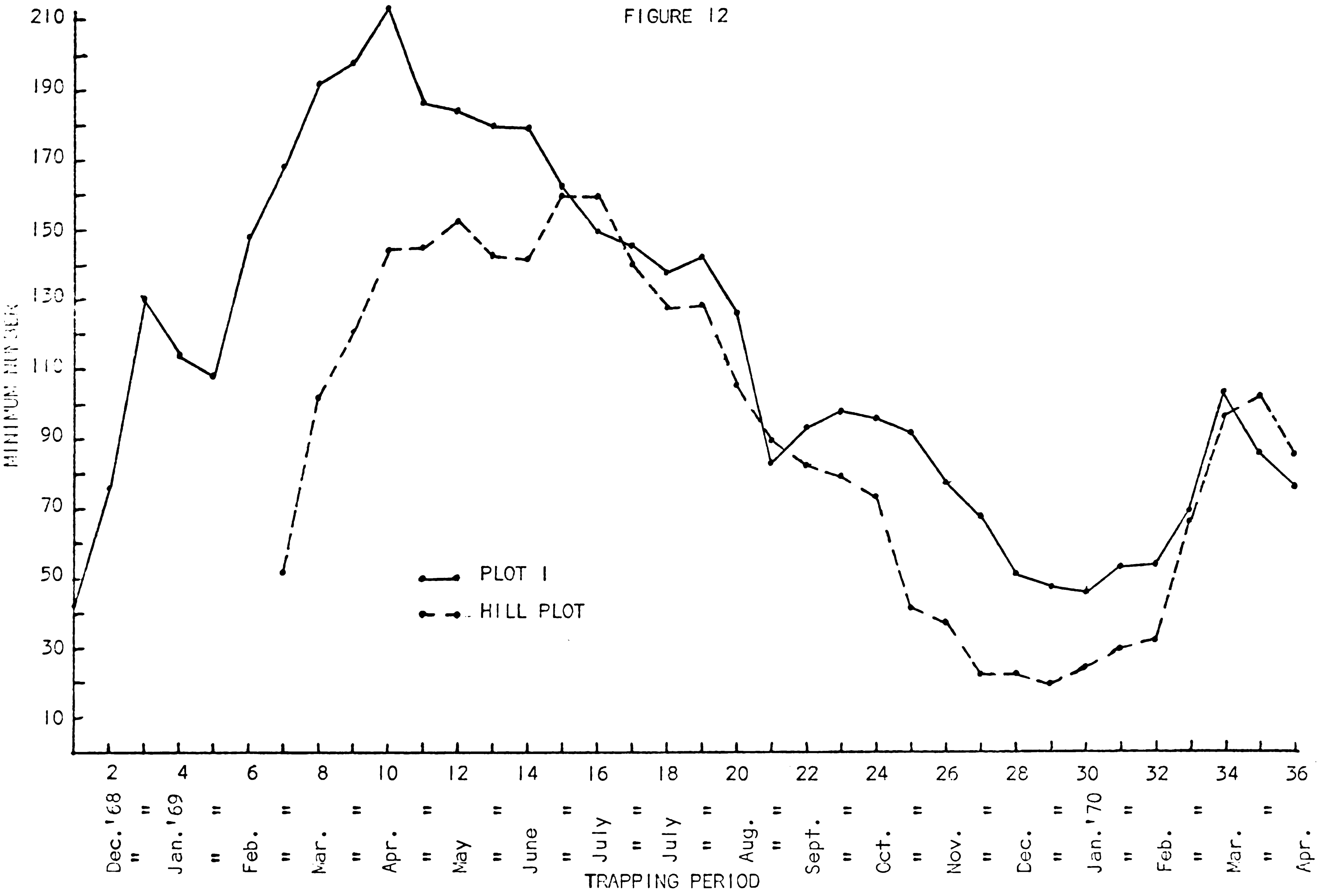
July
July
Aug.
Sept.
Oct.
Nov.
Dec.
Jan.'70
Feb.
Mar.
Apr.

FIGURE 12


MINIMUM NUMBER
210
190
170
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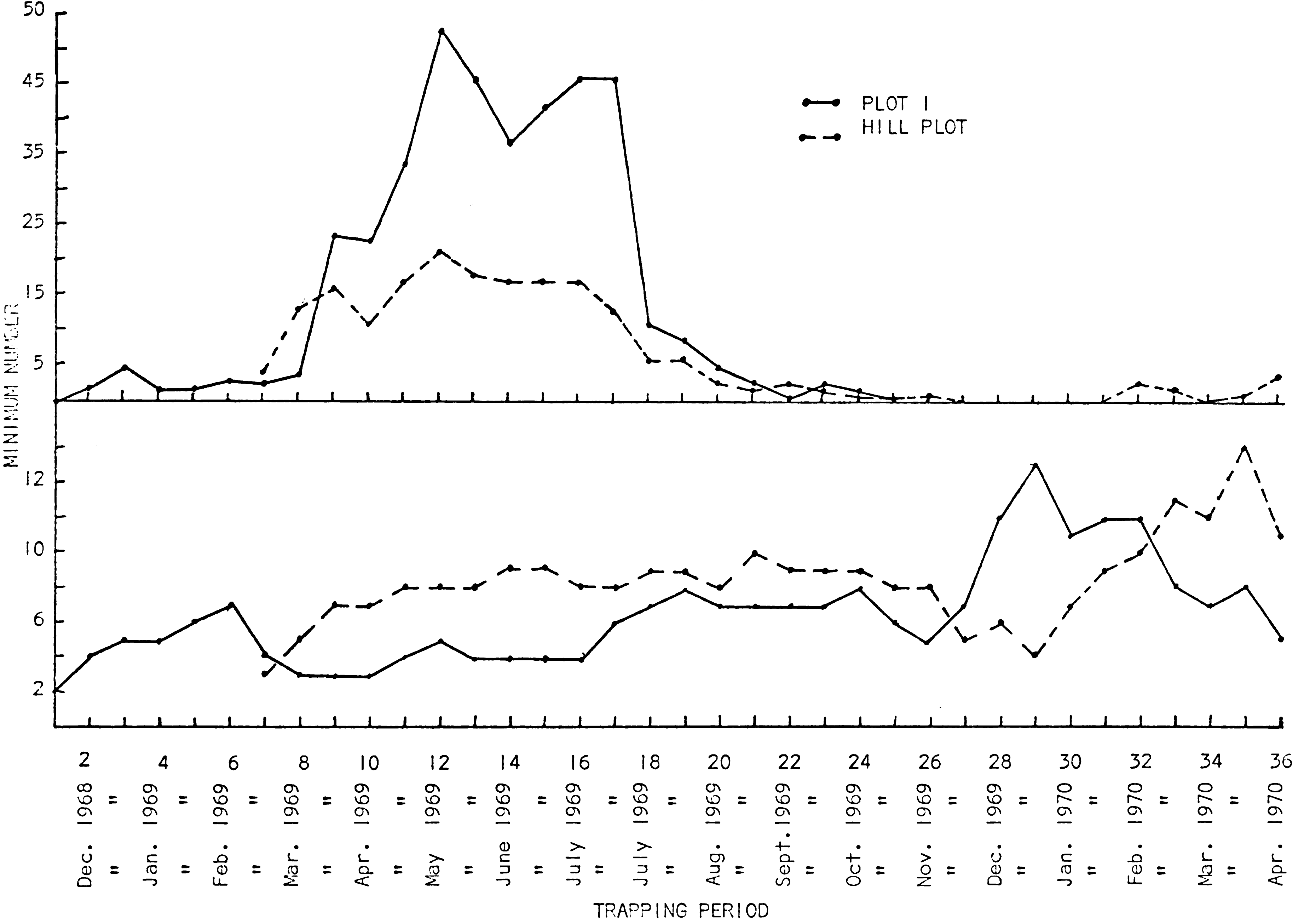
Apr.
TRAPPING PERIOD
PLOT I
HILL PLOT

Figure 13. Minimum number estimates of *Oryzomys nigripes* (top) and *Oxymycteris rutilans* (bottom) in Plot I and Hill Plot.

FIGURE 13


50
45
35
25
15
5
12
10
6
2
MINIMUM NUMBER
PLOT I
HILL PLOT
2
4
6
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36
Dec. 1968
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Jan. 1969
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Feb. 1969
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May 1969
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July 1969
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Dec. 1969
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Jan. 1970
"
Feb. 1970
"
Mar. 1970
"
Apr. 1970
TRAPPING PERIOD

collecting period. In order to determine if actively reproducing females weighed significantly different from others merely perforate, weights for the former were taken, when possible, within one or two periods (sometimes more if the animal was an adult whose weight appeared to change little through time) before or after the pregnant recording.

In Appendix A, weights at which laboratory reproductive maturity occurred for each of the three species are given. In review, adult *A. azarae* were those weighing 18 g or more, for *O. nigripes*, 11 g or more, and for *O. rutilans*, 48 g or more. However, examination of the data showed that very few of the animals in the field reached reproductive condition in the same weight class as determined for the laboratory colony.

Whereas sexual maturity may result at a relatively early age (light weight), older (heavier) animals are the most reproductively active. The average weight found for scrotal *A. azarae* in Plot I was 32.5 ± 5.5 g (N=258) with a range of 17-45; and for Hill Plot, 33.7 ± 6.7 g (N=60) with a range of 16-45 g. Perforate *A. azarae* females for Plot I averaged 24.2 ± 5.2 g (N=227) with a range of 10-40 g, while Hill Plot females averaged 24.9 ± 6.9 g (N=45) with a range of 15-42 g. Females which had experienced recent pregnancies averaged several grams heavier than perforate individuals. Plot I females averaged 26.7 ± 3.7 g (N=127) with a range of 15-37 g, while those from Hill Plot weighed 27.4 ± 4.8 g (N=36), with a range of 19-36 g. There were no significant differences ($p > .05$) in the means of like sex between study sites. Similarly, male-male and female-female mean comparisons within Plot I for the two reproductive periods (1-6; the second period was slightly longer, 24-32, to increase sample size) showed no significant differences. When the mean weights of scrotal males were compared to those of perforate or recently pregnant females, the former were found to be significantly heavier ($p<.05$), although both sets of females were not significantly different from each other.

The reproductive *A. azarae* in the field sites were obviously much larger, heavier and older than the 12-week-old animals from the laboratory (for lab data, see Table A-3). Mice snap-trapped in surrounding areas showed that male *A. azarae* (N=57) in the 31-34 g (near the average weight found for scrotal males in live-trapped plots) weight class averaged (to nearest mm), in body measurements: total length, 185; tail length, 74; head and body length, 111; foot length, 21; and ear length, 13. For females (N=65) in the 23-26 g weight class, these measurements respectively are 171, 69, 103, 20 and 13.

The smaller populations of *O. nigripes* and *O. rutilans* did not lend themselves well to some of the above analyses. For the former species, scrotal males (N=26, both plots pooled) weighed 21.2 ± 4.0 g with a range or 13-27 g while perforate females (N=8, both plots pooled, and including four captured elsewhere on Crovetto Field) weighed 17.6 ± 4.4 g with a range of 9-22 g. No weights for pregnant mice were recorded. In contrast to the significant differences in average weights between scrotal and perforate *A. azarae*, no difference ($p>.05$) was found in *O. nigripes*.

Scrotal males of *O. rutilans*, pooled from both study sites, weighed 92.4 ± 14.1 g (N=82), with a range of 62-125 g while perforate females were less, 76.2 ± 16.0 g (N=39), with a range of 46-110 g. However, this difference was not significant at the .05 level, nor was there any difference between the samples from Plot I and Hill Plot. Pooled females which were known to have been pregnant averaged heavier (85.8 ± 13.9 g) than perforate females, but again this difference was not significant.

As with the reproductive A. azarae, reproductively active O. nigripes and O. rutilans in the field sites were obviously much larger and older than the 12-week-old animals from the laboratory (for lab data, see Table A-4). Oryzomys nigripes snap-trapped in surrounding areas show that males (N=6) in the 20-23 g weight class average (to nearest mm), in body measurements: total length 216; tail length, 118; body length, 97; foot length, 26; and ear length, 13. Females (N=8) in the 16-19 g weight class measure, respectively, 204, 109, 94, 25, and 13. Oxymycteris rutilans males (N=11, 3 with incomplete tails) in the 85-99 g weight class averaged 256, 100, 157, 30, and 18, while females (N=5, 4 with incomplete tails) in the 79-84 g class averaged 255, 100, 158, 30, and 17, respectively.

Length of breeding season

The annual cycles of breeding for A. azarae, O. nigripes, and O. rutilans were measured by presence or absence of females with palpable-sized embryos and/or perforate vaginas, and in the case of males, scrotal testes.

Akodon azarae showed a definite reproductive seasonal trend (Tables 13, 16, 17). The 1968-1969 breeding season was underway before the two field sites were established. The presence of embryos, marking the onset of breeding the following season (1969-1970), was first noted on trap period 25 (first week of November) in both plots. However, perforate females were first detected seven periods (but not to any degree until two periods) earlier in Plot I, and two earlier in Hill Plot. Scrotal males were first observed in both sites three periods before the first embryos were detected.

The first breeding season for _A. azarae_ ended at period 10 (9-14 April, 1969) for both sites, as no embryos were found after this date. The presence of scrotal males ended that same period in Plot I, but continued for several more trapping periods in Hill Plot. The last embryos palpated in the second breeding season were found in period 36 (4-9 April, 1970) and period 34 (12-14 March, 1970) for Hill Plot. The percent of perforate females at both study sites was much less than during the comparable period of the previous breeding season. A few females were still pregnant while the female population as a whole was totally imperforate. Scrotal males were still present in Plot I at the last trapping period, while none was found in Hill Plot after period 34.

Embryo detection then, appears to be much more reliable than scrotal and vaginal changes. The approximate length of the breeding season for _A. azarae_ in the Balcarce area extended from the last of October and first week of November to the middle of April, a period of about 5.5 months.

The number of times a female can produce litters per breeding season, and the contribution made by the young of the year during that breeding season are difficult parameters of reproduction to measure. Some information is supplied by data from the Hill Plot.

From November 1969 to March 1970 (trapping periods 25-34), 28 females produced young 42 times. Nineteen were found pregnant only one time, eight were pregnant two times, one was found pregnant three times, and one was recorded pregnant four times. Based upon palpation data, reproductive animals gave birth to approximately 200 young during the

Table 13. Intensity of breeding in *Akodon azarae*, Plot I and Hill Plot (in parentheses), as measured by the number of pregnant females determined by palpation, the percentage of pregnancy of the adult females and all age class females, and the number of litters and average litter size counted by palpation.

TRAP PERIOD	NO. PREG.	% ADULT PREG.	% TOTAL PREG.	NO. LITTERS PALPATED	AVG. LITTER SIZE
1 Dec. 1968	9	52.9	40.9	9	4.2
2 " "	16	50.0	40.0	14	4.7
3 Jan. 1969	23	43.4	29.1	22	4.3
4 " "	10	28.6	17.0	8	4.0
5 " "	8	29.6	19.1	7	4.6
6 Feb. "	8	23.5	12.7	5	3.2
7 " "	12(3)	30.0(60.0)	23.1(23.1)	8(3)	4.9(3.7)
8 Mar. "	3(3)	6.0(27.3)	4.1(9.7)	1(1)	5.0(5.0)
9 " "	2(1)	4.3(4.6)	3.2(3.7)	2(1)	3.0(4.0)
10 Apr. "	1(1)	1.5(3.1)	1.3(2.1)	1	3.0
11 " "					
12 May "					
13 " "					
14 June "					
15 " "					
16 July "					
17 " "			No Pregnancies Detected Here.		
18 " "					
19 Aug. "					
20 " "					
21 Sept. "					
22 " "					
23 Oct. "					
24 " "					
25 Nov. "	4(2)	10.0(15.4)	10.0(15.4)	2(1)	5.0(4.0)
26 " "	5(5)	20.8(38.5)	20.8(38.5)	1(4)	5.0(4.8)
27 Dec. "	11(4)	45.8(50.0)	45.8(50.0)	6(2)	4.5(5.5)
28 " "	7(3)	35.0(42.9)	31.8(37.5)	2(1)	4.5(6.0)
29 Jan. 1970	4(2)	26.7(33.3)	23.5(25.0)	2(2)	3.5(4.0)
30 " "	1(7)	8.3(53.9)	6.3(53.9)	(4)	(5.5)
31 " "	11(3)	64.7(23.1)	50.0(23.1)	5(2)	3.8(5.5)
32 Feb. "	7(8)	46.7(57.1)	43.8(47.1)	3(3)	4.3(5.0)
33 " "	9(3)	36.0(30.0)	28.1(14.3)	6(1)	3.8(5.0)
34 Mar. "	8(6)	25.8(35.3)	17.4(24.0)	3(2)	5.0(3.5)
35 " "	2	8.7	6.7	1	1.0
36 Apr. "	1	3.2	2.6		

Table 14. Intensity of breeding in *Oryzomys nigripes*, Plot I and Hill Plot (data combined), as measured by the number of pregnant females determined by palpation, the percentage of pregnancy of the adult females and all age class females, and the number of litters as counted by palpation.

TRAP PERIOD	NO. PREG.	% ADULT* PREG.	% TOTAL PREG.	NO. LITTERS PALPATED	AVG. LITTER SIZE
1 Dec. '68					
2 " "					
3 Jan. '69	1	50.0	50.0	1	4.0
4 " "					
5 " "					
6 Feb. "					
7 " "	2	100.0	100.0	2	4.0
8 Mar. "	1	50.0	50.0		
9 " "	1	12.5	11.1		
10 Apr. "	1	16.7	14.3	1	6.0
11 " "	1	16.7	16.7		
12 May "	2	11.8	11.8	1	3.0
13 " "					
14 Jun. "					
15 " "					
16 July "					
17 " "					
18 " "					
19 Aug. "					
20 " "	1	50.0	50.0	1	1.0
21 Sept. "					
22 " "					
23 Oct. "					
24 " "					
25 Nov. "	Last week *Oryzomys nigripes* recorded for Plot I.				
26 " "					
27 Dec. "					
28 " "					
29 Jan. '70					
30 " "					
31 " "					
32 Feb "	2	100.0	100.0	1	3.0
33 " "					
34 Mar "					
35 " "					
36 Apr. "					

*No subadults were found pregnant.

Table 15. Intensity of breeding in *Oxymycteris rutilans*, Plot I and Hill Plot (data combined), as measured by the number of pregnant females determined by palpation, the percentage of pregnancy of the adult females and all age class females, and the number of litters and average litter size as counted by palpation.

TRAP PERIOD	NO. PREG.	% ADULT* PREG.	% TOTAL PREG.	NO. LITTERS PALPATED	AVG. LITTER SIZE
1 Dec. '68					
2 " "	2	100.00	100.0	2	3.0
3 Jan. '69	1	50.00	50.0	1	4.0
4 " "	2	66.7	66.7	2	4.5
5 " "	1	50.0	33.3		
6 Feb. "					
7 " "					
8 Mar. "					
9 " "					
10 Apr. "	1	25.0	25.0	1	4.0
11 " "					
12 May "	2	50.0	50.0	2	3.0
13 " "					
14 June "					
15 " "	1	50.0	50.0		
16 July "					
17 " "	1	50.0	50.0	1	3.0
18 " "	1	33.3	33.3		
19 Aug. "	2	33.3	33.3	1	3.0
20 " "					
21 Sept. "					
22 " "	4	50.0	40.0	2	3.0
23 Oct. "	2	40.0	40.0	1	3.0
24 " "	1	16.7	16.7	1	4.0
25 Nov. "	2	66.7	66.7	1	4.0
26 " "	2	40.0	40.0		
27 Dec. "	3	75.0	42.9	1	3.0
28 " "	6	60.0	54.5	3	3.7
29 Jan. '70	1	33.3	16.7		
30 " "	1	100.0	33.3		
31 " "	3	50.0	33.3	1	6.0
32 Feb. "	3	33.3	27.3		
33 " "	3	42.9	30.0		
34 Mar. "	1	25.0	25.0	1	2.0
35 " "	1	50.0	12.5		
36 Apr. "	2	33.3	28.6	1	2.0

*No subadults were found pregnant, and only three females from Hill Plot were discovered to be pregnant.

5-6 month breeding season. Plot I A. azarae during this same season produced about 130 young, compared to over 330 produced the high density season, not counting the breeding prior to early December when the study began.

Oryzomys nigripes did not produce young until later in the summer season, then remained in reproductive condition during early fall (Table 14, 18). No young were palpated until trap period 3, (1-3 Jan., 1969) during the first summer, and period 32 (11-13 Feb., 1970), the second summer. Scrotal males were common at the onset of the study the first summer and were first evident in period 26 (20-22 Nov., 1969) of the second summer. Perforate females were too few to allow any conclusions. The last of the season were palpated in period 12 (9-11 May, 1969). One female was thought to be pregnant during late winter (last of August), with one embryo. When brought to the lab, then checked several days later, there was no evidence of pregnancy. Scrotal males were not found after trap period 13 (25-27 May, 1969). The reproductive season it appears, extended for at least 4.5 months, and possibly longer.

Unlike the former two species, O. rutilans were found in reproductive condition in all seasons of the year (Tables 15, 18). Embryos were detected in nearly every month, as were scrotal males and perforate females.

An analysis of Hill Plot O. rutilans natality showed that 10 females were discovered pregnant 26 times during a 12 month period starting with period 10. One of these animals was found pregnant seven times; one, four times; two, three times; one, two times; and four, one time. With an average litter size of approximately 3.1, this resulted in the production of about 81 young during that year. Slightly fewer, 76, were recorded during the time Plot I was in operation.

Intensity of breeding

Observing changes in pregnancy rates, percentage of perforate (or if a male, scrotal) animals in the population are methods of determining at what period of the annual breeding cycle reproduction is most intense. In addition, species specific breeding strategies, and multi-annual population flucuations can also be examined by means of these parameters.

Akodon azarae, judging only from Plot I, did not undergo any change during the two breeding seasons in the percent of pregnant females (Table 16). The 1968-1969 breeding season might be expected to produce a larger proportion of pregnant females in Plot I because of the plentiful cover and abundant forage. However, if the 1968-1969 breeding season is compared with the same time the following year (27-32), there is no difference in the average percent (approximately 38 percent) of pregnant females in the adult population. Yet, comparing these same two periods, over twice as many females were pregnant the first season, suggesting that mortality and/or emigration are having an effect (discussed later) in reducing the population density from its first season high. This is also suggested by the fact that the intensity of breeding among the total female population decreased for a time (periods 1-6, Table 13) as young animals entered the trappable population, but did not reach reproductive condition until somewhat later. This is in contrast to comparable periods in the second season (periods 27-32) where there is little difference between the percent of adult females pregnant and the percent of total females pregnant, thus demonstrating

that young animals made up only a very small portion of the total population the second season.

Based on the above observations, the first breeding season for A. azarae may have begun somewhat earlier in Plot I since there was already approximately a 10 percent difference between the two female groups by the first period, but only a 3 percent difference by the comparable date (period 27) in the second season. Unfortunately, the study site was not begun early enough to verify the commencement of breeding. It can only be stated that breeding terminated the same time in both seasons.

The intensity of breeding in A. azarae females, as detected by the proportion of perforate individuals in the population (Table 16, 17), definitely shows a higher reproductive intensity at a high population (first season). Not only are more adult females perforate but a number of subadults and juveniles also were perforate, a condition which did not manifest itself the second season in the latter two age groups. Male scrotal development showed little change during the two seasons. During the two reproductive seasons (periods 1-6 and 27-32) in which the females were examined, the proportion of total adult scrotal males in each season did not differ more than an average four percent (63, 67 percent, Plot I).

Limited data are available for the other two species. Oryzomys nigripes reproduction (Tables 14, 18) only occurred in Plot I the first year, after which the population steadily declined and never reappeared. The data also suggest that the main peak of reproduction is slightly later in the year than that found for A. azarae. The intensity of breeding by O. rutilans (Tables 15, 18) showed little seasonal difference in reproductive performance. However, of 29 periods (out of a possible 30)

Table 16. Intensity of breeding in Akodon azarae, Plot I, as measured by the presence of a well-developed scrotum in males and a perforate vagina in females. Under each age heading and trapping period are given the number of animals captured, the number perforate or scrotal, and the proportion of the age group which show that condition.

	Males			Females		
Trap Period	Juv.	SA	Adult	Juv.	SA	Adult
1Dec. '68	3(0)	3(0)	15(14).93	4(0)	1(0)	17(5).29
2 " "	2(0)	4(0)	20(18).90	3(1).33	5(3).60	32(23).72
3Jan. '69	2(0)	15(0)	23(7).30	10(1).10	16(3).19	53(40).75
4 " "	2(0)	9(0)	16(10).63	3(0)	21(4).19	35(31).89
5 " "	9(0)	11(1).09	19(12).63	7(0)	8(0)	27(25).93
6Feb. "		21(0)	39(14).36	7(0)	22(3).14	34(22).65
7 " "	1(0)	9(0)	56(9).16		12(0)	40(24).60
8Mar. "	2(0)	13(0)	58(8).14		23(2).09	50(24).48
9 " "	2(0)	6(0)	58(5).09	4(0)	12(2).17	47(7).15
10Apr. "		7(0)	61(2).03	2(0)	10(0)	66(1).02
11 " "		5(0)	69(0)	1(0)	6(0)	46(0)
12May "		2(0)	59(0)		7(0)	43(0)
13 " "		2(0)	43(0)		2(0)	37(0)
14June "			56(0)		2(0)	53(1).02
15 " "			50(1).02		3(0)	46(0)
16July "		1(0)	44(0)			40(0)
17 " "		4(0)	47(0)		3(0)	39(0)
18 " "			59(1).02		2(1).50	48(1).02
19Aug. "			53(0)		4(2).50	50(1).02
20 " "			50(0)		2(0)	50(3).06
21Sept. "			36(0)			25(0)
22 " "			44(7).16		4(1).25	23(1).04
23Oct. "			45(1).02		4(2).50	32(12).38
24 " "			43(6).14			32(19).59
25Nov. "			38(12).32			40(17).43
26 " "	1(0)		34(22).65			24(8).33
27Dec. "	1(0)	1(0)	31(19).61			24(4).17
28 " "			18(12).67	2(0)		20(1).05
29Jan. '70	4(0)	1(0)	15(12).80	1(0)	1(0)	15(2).13
30 " "	2(0)	3(0)	9(4).44		4(0)	12(0)
31 " "		4(0)	14(11).79	1(0)	4(1)	17(4).24
32Feb. "		1(0)	18(13).72		1(0)	15(1).07
33 " "		4(1).25	22(15).68	1(0)	6(0)	25(3).12
34Mar. "	1(0)	7(0)	38(10).26	1(0)	14(0)	31(0)
35 " "	1(0)	4(0)	33(7).21		7(0)	23(3).13
36Apr. "	1(0)	2(0)	36(8).22		7(0)	31(0)

Table 17. Intensity of breeding in Akodon azarae, Hill Plot, as measured by the presence of a well-developed scrotum in males and a perforate vagina in females. Under each age heading and trapping period are given the number of animals captured, the number perforate or scrotal, and the percentage of the age group which show that condition.

	MALES			FEMALES		
TRAP PERIOD	Juvenile	SA	Adult	Juvenile	SA	Adult
1 Dec. '68						
2 " "						
3 Jan. '69						
4 " "						
5 " "						
6 Feb. "						
7 " "	3(0)	17(0)	19(4) 21	1(0)	7(2)29	5(5)100
8 Mar. "		21(2)10	37(2) 05	3(1)33	17(4)24	11(5) 45
9 " "		8(0)	48(0)		5(0)	22(3) 14
10 Apr. "		10(0)	46(1) 02	2(0)	13(0)	32(4) 13
11 " "	1(0)	5(0)	48(1) 02		13(0)	36(0)
12 May "	2(0)	8(1)13	60(1) 02		11(0)	35(0)
13 " "		3(0)	53(0)		6(0)	39(0)
14 June "		1(0)	62(2) 03		1(0)	50(0)
15 " "		3(0)	69(0)		7(0)	48(0)
16 July "		4(0)	64(0)		8(0)	45(0)
17 " "		4(0)	65(0)		5(0)	38(0)
18 " "			49(0)			29(0)
19 Aug. "		1(0)	57(0)		10(0)	32(0)
20 " "		1(0)	46(0)		2(0)	30(1)
21 Sept. "		1(0)	34(0)		1(0)	27(0)
22 " "			37(1) 03		1(0)	32(0)
23 Oct. "			41(1) 02		3(0)	30(1) 03
24 " "			36(4) 11		1(0)	29(9) 31
25 Nov. "			23(7) 30			13(3) 23
26 " "			18(7) 39			13(0)
27 Dec. "			6(5) 83			8(1) 13
28 " "		1(0)	6(2) 33		1(0)	7(1) 14
29 Jan. '70			4(4)100	1(0)	1(0)	6(1) 17
30 " "		1(0)	3(3)100			13(1) 08
31 " "	1(0)	4(0)	6(3) 50			13(1) 08
32 Feb. "		2(0)	9(4) 44	2(0)	1(0)	14(2) 14
33 " "	5(0)	13(0)	19(4) 21	2(0)	9(0)	10(0)
34 Mar. "	1(0)	5(0)	40(2) 05	1(0)	7(0)	17(0)
35 " "		16(0)	31(0)		16(0)	19(0)
36 Apr. "	1(0)	11(0)	37(0)		16(0)	21(0)

Table 18. Intensity of breeding in *Oryzomys nigripes* and *Oxymycteris rutilans*, Plot I and Hill Plot (data combined), as indicated by the number of young animals captured (SA = subadults) and sexual condition (testes scrotal, vagina perforate). The first column in each class gives the total number captured; the second (in parentheses) the number showing the sexual condition; and in the third column, the percent showing the sexual condition.

	Oryzomys nigripes				*Oxymycteris rutilans*			
TRAP PERIOD	MALES		FEMALES		MALES		FEMALES	
	SA	Adults	SA	Adults	SA	Adults	SA	Adults
1 Dec. '68						2(2)100		
2 " "		1(1)100		1(0)		1(1)100		2(1) 50
3 Jan. '69		4(3) 75		2(0)		1(1)100		2(2)100
4 " "						2(1) 50		3(3)100
5 " "						2(2)100	2(1)50	2(1) 50
6 Feb. "		1(1)100			1(0)	3(1) 33		2(2)100
7 " "	1(0)	2(1) 50		2(0)		2(1) 50		2(2)100
8 Mar. "		12(1) 9		2(1) 50		3(3)100		3(3)100
9 " "	1(0)	24(8) 33	1(1)100	9(1) 11		2(2)100	1(0)	4(0)
10 Apr. "		10(1) 10	1(0)	10(0)		2(1) 50		4(0)
11 " "	2(0)	25(5) 20	1(0)	8(0)		3(2) 67		5(2) 40
12 May "		43(5) 12	1(0)	22(1) 5	1(0)	2(1) 50		4(0)
13 " "	1(0)	34(1) 3		15(1) 7		2(1) 50		5(0)
14 June "		14(0)		10(0)		2(2)100		4(1) 25
15 " "		23(0)		19(0)		3(3)100		9(2) 22
16 July "		28(0)		20(0)		2(1) 50		4(0)
17 " "		31(0)		24(0)		3(3)100		5(2) 40
18 " "		11(0)		4(0)		5(5)100		8(4) 50
19 Aug. "		10(0)		7(0)		5(5)100		11(2) 18
20 " "		3(0)		2(1) 50		4(3) 75		8(2) 25
21 Sept. "		3(0)			1(0)	5(5)100	**	8(2) 25
22 " "		2(0)		1(0)		4(4)100	2(0)	8(0)
23 Oct. "		2(0)		2(0)	1(0)	6(5) 83		8(4) 50
24 " "		3(0)				5(2) 40		9(4) 44
25 Nov. "		*2(0)				3(3)100		3(0)
26 " "		1(1)100				3(3)100		5(0)
27 Dec. "							3(0)	4(2) 50
28 " "						4(1) 25	1(0)	10(0)
29 Jan. '70					3(0)	5(0)	3(0)	3(2) 67
30 " "						5(1) 20	2(0)	2(0)
31 " "					1(0)	4(4)100	3(0)	6(0)
32 Feb. "		1(1)100		2(1) 50	1(0)	7(4) 57	2(0)	9(1) 11
33 " "		2(1) 50			1(0)	3(2) 67	3(0)	7(3) 43
34 Mar. "						6(4) 67	1(0)	6(0)
35 " "		1(0)			3(0)	6(2) 33	2(0)	6(1) 17
36 Apr.		3(0)		1(0)	1(0)	6(2) 33	1(0)	8(1) 13

*No *O. nigripes* in Plot I after this date.
**Juvenile captured here.

in which Plot II adult females were found, only 14 percent were in the perforate condition, compared to 39 percent for 20 periods in Plot I during the same 30 period time span. In direct contrast to this, the number of pregnant females was 2.4 times (12) higher in Hill Plot than that (5) for Plot I.

Survival

Minimum survival rates

The minimum survival rate is here defined as that proportion of the trappable population, which when marked at time t will still be in the study plot at t + 1. If captured after, but not at t + 1, the animal is presumed to have been on the plot at t + 1 and is added to that total. A number of authors (Newson and Chitty, 1962; Krebs, 1964; Krebs 1966; Krebs *et al.*, 1969) have recognized that their survival rates reflect not only mortality factors but also the possible unequal effects of immigration and emigration from the study area. As Krebs (1966) stated, the data are expressed as minimum survival rates between trapping periods (14 days in this study). The true survival rate should never be less than this rate.

Minimum survival rates (Table 19) for *A. azarae*, sexes and ages pooled, suggest that there was a noticeable change between reproductive and non-reproductive seasons. This is true especially in Plot I where each reproductive season averaged 72-73 percent, and the non-reproductive season, 83 percent. On Hill Plot, the winter survival rate averaged 80 percent, but only slightly lower, 79.5 percent for the first reproductive season, and much lower, 59 percent, for the second reproductive season.

On the same table, *O. nigripes* (plots pooled) show a much lower

Table 19. Minimum survival rates per 14 days for *Akodon azarae*, *Oryzomys nigripes* and *Oxymycteris rutilans*. Total catch released is in parentheses, followed by the total number of the same animals captured in subsequent trapping periods.

TRAP PERIOD	AKODON AZARAE Plot I	 Hill Plot	ORYZOMYS NIGRIPES Plots Pooled	OXYMYCTERIS RUTILANS Plots Pooled
1 Dec. '68				
2 " "	.72(43) 31			.50(2) 1
3 Jan. '69	.69(64) 44		.00(1) 0	1.00(3) 3
4 " "	.55(107) 59		.00(4) 0	.67(3) 2
5 " "	.69(80) 55			.75(4) 3
6 Feb. "	.77(70) 54			.60(5) 3
7 " "	.84(120) 101		1.00(1) 1	.50(6) 3
8 Mar. "	.83(115) 95	.84(51) 43	.80(5) 4	.75(4) 3
9 " "	.72(139) 100	.75(89) 67	.54(13) 7	1.00(6) 6
10 Apr. "	.76(128) 97	.83(83) 69	.43(23) 13	.83(6) 5
11 " "	.62(145) 90	.76(103) 78	.89(18) 16	1.00(6) 6
12 May "	.90(126) 113	.82(103) 84	.75(32) 24	.88(8) 7
13 " "	.85(111) 94	.81(117) 95	.76(38) 29	1.00(6) 6
14 June "	.89(83) 74	.89(100) 89	.88(43) 30	1.00(7) 7
15 " "	.78(110) 86	.88(114) 100	.76(21) 16	1.00(6) 6
16 July "	.82(198) 80	.82(127) 104	.59(39) 23	.91(11) 10
17 " "	.89(183) 74	.83(121) 100	.52(44) 23	1.00(6) 6
18 " "	.85(192) 78	.87(112) 97	.21(53) 11	1.00(8) 8
19 Aug. "	.90(109) 98	.86(78) 67	.33(15) 5	.92(12) 11
20 " "	.73(106) 77	.73(98) 72	.29(17) 5	.87(15) 13
21 Sept. "	.41(100) 41	.72(79) 57	.17(6) 1	.82(11) 9
22 " "	.84(61) 51	.83(63) 52	.33(3) 1	.85(13) 11
23 Oct. "	.94(71) 62	.86(70) 60	.33(3) 1	.92(13) 12
24 " "	.90(79) 71	.78(73) 57	.50(4) 2	.86(14) 12
25 Nov. "	.87(75) 65	.49(57) 28	.33(3) 1	.80(15) 12
26 " "	.77(78) 60	.69(36) 25	.00(2) 0	.83(6) 5
27 Dec. "	.78(58) 45	.53(30) 16	.00(1) 0	.57(7) 4
28 " "	.61(57) 35	.54(13) 7		.86(7) 6
29 Jan. '70	.65(40) 26	.47(15) 7		.60(15) 9
30 " "	.79(34) 27	.80(10) 8		.69(13) 9
31 " "	.73(30) 22	.53(17) 9		.50(8) 4
32 Feb. "	.80(40) 32	.58(24) 14		.80(15) 12
33 " "	.74(35) 26	.64(28) 18	.00(3) 0	.68(19) 13
34 Mar. "	.82(57) 47	.75(57) 43	.00(2) 0	.69(13) 9
35 " "	.66(87) 57	.54(71) 38		.83(12) 10
36 Apr. "	.73(66) 48	.40(82) 33	.00(1) 0	.44(16) 7

survival rate, about 58 percent for the periods 9-20, the time when the mice were most abundant. The _O. rutilans_ population (plots pooled) had a survival rate of about 70-76 percent during the summers, but in the winter it rose to 92 percent.

True survival rates

In a series of field experiments with _Microtus pennsylvanicus_ and _M. ochrogaster_, Krebs _et al._ (1969) showed that "survival rates" of these species in large enclosures (where emigration could not take place) were much higher (often over 30 percent higher) than neighboring unenclosed populations. This evidence could indicate that a major portion of the survival rate is lowered simply because of emigratory and immigratory patterns. If it is assumed that these two movements are approximately equal within any given time period, and if one examines a population during a non-reproductive period, the decrease in population from one time period to the next can be a reliable measurement of survivalbility. Because microtines may be in a non-reproductive state for only several months at a time or may breed continuously throughout the year (Krebs, 1966; Krebs _et al._, 1969), this type of analysis for estimating a true survival rate is difficult. _Akodon azarae_ present the opportunity to examine true survival rates since there is a 5-6 month period of non-reproduction (Table 13) during the winter. This estimate is calculated by dividing the minimum number known alive at one trapping period by the number known alive at the next trapping period. The data, presented in Table 20, show that the average estimated true survival rate is between 93-95 percent per 14 days. This is 30-40 percent higher than the minimum survival rate calculated earlier, and as such, is much closer to the values determined for enclosed populations of _Microtus_.

Table 20. True survival rates for *Akodon azarae* during the non-reproductive (winter) season.

	AKODON AZARAE			
	Plot I		Hill Plot	
Trap Period	Survival Rate	Min. No. Alive	Survival Rate	Min. No. Alive
10 Apr. 1969		214		145
11 " "	.87	187	1.00	145
12 May "	.99	185	1.06	153
13 " "	.97	180	.93	143
14 June "	.99	179	.99	142
15 " "	.91	162	1.13	160
16 July "	.93	150	1.00	160
17 " "	.97	146	.88	141
18 " "	.95	139	.91	128
19 Aug. "	1.03	143	1.01	129
20 " "	.89	127	.82	106
21 Sept. "	.65	83	.85	90
22 " "	1.13	94	.92	83
23 Oct. "	1.05	99	.96	80
24 " "	.98	97	.93	74
25 Nov. "	.96	93	.57	42
Average True Survival Rate	$\Sigma 1427$ $N=15$ $\bar{X}=95.1\%$		$\Sigma 1396$ $N=15$ $\bar{X}=93.1\%$	

Movements

The movement patterns of populations are parameters which are affected by density, season, age and sex classes, and interspecific competition. This section examines the movement patterns of the three aforementioned rodent species in an effort to understand how they are affected by the above mentioned variables.

Recaptures per trapping period

The percentage of *A. azarae* which were captured two or three times per three day trapping period is given in Table 21. When sexes and age classes were pooled, an average 42-44 percent (Hill Plot and Plot I, respectively) of the animals were recaptured. The subadult individuals averaged for females, 25 and 37 percent, and males, 40 and 15 percent (Hill Plot and Plot I, respectively). The adults averaged more than this, with males at 43 and 46 percent, and females, 48 and 48 percent (Hill Plot and Plot I, respectively). If the adults are segregated by sex, season, and study plot (Table 23), the percentage of *A. azarae* recaptured show no clear trend from season to season.

Oryzomys nigripes and *O. rutilans* recapture data are much less complete per trap period for parts of the study (Table 22). These two species, sexes pooled, have the Table 22 data grouped according to season and study plot, (Table 24). The data are limited for *O. nigripes*, since they seemed to lead an ephemeral existence in the study sites. The recapture values are rather high when one considers that *A. azarae* had the first opportunity to enter available traps. Data for *O. rutilans* in the above table suggests that when *A. azarae* populations are high, as in Plot I, the former species are captured less frequently than when *A. azarae* populations are down (e.g., Plot I second summer, and Hill

Table 21. Percentage of <u>Akodon azarae</u> which were captured more than once during each trapping period, arranged according to sex, age class, and study plot.

	Subadult Males		Subadult Females		Adult Males		Adult Females		Pooled Sexes and Ages	
TRAP PERIOD	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot
1 Dec. '68	17		00		13		24		17	
2 " "	50		38		45		34		39	
3 Jan. '69	24		19		52		55		42	
4 " "	36		33		44		57		45	
5 " "	30		20		21		59		36	
6 Feb. "	29		10		46		68		41	
7 " "	20	35	83	25	41	42	40	60	36	38
8 Mar. "	20	38	22	40	40	51	36	73	34	48
9 " "	25	38	25	20	33	48	30	23	30	39
10 Apr. "	29	40	25	07	38	41	33	41	34	36
11 " "	20	33	29	38	49	48	43	56	45	49
12 May "	00	10	57	36	36	50	33	51	35	46
13 " "	00	33	00	67	26	47	22	46	23	48
14 June "		100	50	00	38	60	40	68	39	63
15 " "		67	33	00	42	38	43	46	42	39
16 July "	00			50	27	38	23	44	25	40
17 " "	00	50	33	40	40	62	28	61	35	60
18 " "			100		39	47	52	52	46	49
19 Aug. "		100	50	50	36	68	44	56	40	63
20 " "		100	50	00	36	43	58	43	47	43
21 Sept. "				00	42	41	52	33	46	37
22 " "			50	00	66	84	52	69	61	76
23 Oct. "			75	100	76	76	53	73	67	76
24 " "				100	65	64	63	59	64	62
25 Nov. "					53	70	45	69	49	69
26 " "	00				65	56	63	69	63	61
27 Dec. "	00				52	33	58	38	65	36
28 " "		00	100	00	72	33	70	43	73	33
29 Jan. '70	20		50	00	53	00	40	17	43	08
30 " "	20	100	25		78	00	50	77	50	12
31 " "	25	20	60		57	33	82	23	65	25
32 Feb. "	00		00	00	33	22	33	43	31	29
33 " "	00	17	14	09	55	26	44	40	41	22
34 Mar. "	00	17	13	00	42	20	55	35	38	21
35 " "	20	06	29	06	39	23	57	21	43	16
36 Apr. "	00	08	14	19	61	30	78	24	53	23

Table 22. Percentage of *Oryzomys nigripes* and *Oxymycteris rutilans*, which were captured more than once during each trapping period, and arranged with sex and age classes pooled for each study plot.

	Oryzomys nigripes		*Oxymycteris rutilans*	
Trap Period	Plot I	Hill Plot	Plot I	Hill Plot
1 Dec '68			00	
2 " "	00		00	
3 Jan '69	33		33	
4 " "			80	
5 " "			20	
6 Feb "	00		33	
7 " "	00	25	00	33
8 Mar "	00	17	00	80
9 " "	07	09		50
10 Apr "	00	00		33
11 " "	21	29	00	71
12 May "	19	17	00	00
13 " "	22	57	00	67
14 Jun "	38	43		83
15 " "	21	17	00	67
16 July "	33	46		33
17 " "	35	60	00	80
18 " "	43	00	20	29
19 Aug "	54	25	29	38
20 " "	40	100	67	75
21 Sept "	33	50	60	11
22 " "	100	50	00	56
23 Oct "	100	00	40	44
24 " "	50	100	29	63
25 Nov "	100		00	80
26 " "		00		38
27 Dec "			00	50
28 " "			60	40
29 Jan '70			38	
30 " "			33	00
31 " "			10	00
32 Feb "		00	50	11
33 " "		00	17	25
34 Mar "			40	38
35 " "		00	20	33
36 Apr "		00	60	00

Table 23. The proportion of recaptured adult *Akodon azarae* segregated by sex, plot, and season. Proportion is the average of appropriate data shown in Table 21. Numbers in parentheses show average number of individuals captured each period.

	Adult Males		Adult Females	
	Plot I	Hill Plot	Plot I	Hill Plot
First Summer Periods 1-10	.37 (37)	.46 (38)	.44 (40)	.49 (18)
Winter Periods 11-24	.44 (50)	.55 (52)	.43 (40)	.54 (36)
Second Summer Periods 25-34	.56 (24)	.36 (11)	.54 (22)	.45 (11)

Table 24. The proportion of recaptured *Oryzomys nigripes* and *Oxymycteris rutilans*, sexes and ages pooled, and segregated by plot and season. Proportion is the average of appropriate data shown in Table 22. Numbers in parentheses show average number of individuals captured each period.

	Oryzomys nigripes		*Oxymycteris rutilans*	
	Plot I	Hill Plot	Plot I	Hill Plot
First Summer (Periods 1-10)	-	-	.21 (3)	.49 (5)
Winter (Periods 11-24)	.44 (18)	.42 (11)	.20 (4)	.51 (7)
Second Summer (Periods 25-34)	-	-	.36 (7)	.31 (6)

Plot first summer and winter).

Spatial distribution-centers of activity

It is the proportion of animals taken more than once during each trapping period that forms the basis for the movement analysis. The center of activity (Hayne, 1949) was calculated for each animal during each trapping period. From this point, all distances to points of recapture was measured, and average values were then calculated for each recaptured individual. In those instances where circular home range data are desired, the mean distance serves as the radius.

The spatial distribution, utilizing the centers of activity, was determined for each species by dividing Plot I and Hill Plot into four quadrants (Figure 2, 9). The number of animals captured each trapping period for individual quadrants was then averaged for each season (Table 25).

The data for A. azarae show that for Plot I, mouse density remained highest five out of six times in Quadrants A and B. It was in these two quadrants where vegetation cover and density values were highest (Figure 3 shows an area within A-B, Figure 7 for C-D). On Hill Plot, the most heterogeneous of the four quadrants, Quadrant A showed the highest densities at all seasons. A somewhat unexpected result was the rather high values in Quadrants C-D, both of which were covered rather homogeneously with stands of Paspalum quadrifarium (Figure 9), a plant of questionable nutritive value (Caswell et al., 1973), but possibly offering excellent concealment advantages. Density figures for Hill Plot quadrants show lower values than Plot I for the first summer, with winter values more equal to those of Plot I winter (note that Hill Plot winter density is higher than summer density, contrary to that found in

Table 25. Average number of _Akodon azarae_, _Oryzomys nigripes_, and _Oxymycteris rutilans_ captured each trapping period for individual quadrants in Plot I and Hill Plot.*

	PLOT I			HILL PLOT		
	1st Summer (Per. 1-10)	Winter (Per. 11-24)	2nd Summer (Per. 25-34)	1st Summer (Per. 7-10)	Winter (Per. 11-24)	2nd Summer (Per. 25-34)
			AKODON	AZARAE		
Quadrant A	30.5	27.6	17.1	23.3	28.2	10.1
" B	28.1	27.3	12.1	21.4	25.4	6.6
" C	23.5	21.1	9.7	19.9	20.1	6.8
" D	24.2	17.9	13.8	20.8	20.9	7.2
			ORYZOMYS	NIGRIPES		
Quadrant A	0.9	4.5	0.5	1.3	1.3	0.7
" B	1.6	3.7	-	1.3	0.6	1.0
" C	2.6	5.8	-	3.0	2.1	1.3
" D	1.9	3.7	0.5	2.3	3.6	0.7
			OXYMYCTERIS	RUTILANS		
Quadrant A	0.5	0.5	2.4	0.4	2.5	2.9
" B	2.0	1.3	0.9	2.0	1.7	0.4
" C	0.4	0.8	0.8	1.3	2.1	0.9
" D	0.4	1.2	3.5	1.4	1.1	1.8

*If no individuals of a species were captured on a study plot during a specific trapping period, then that period was not used when calculating the average number.

Plot I). Second summer values were much lower than first summer values in both plots.

Spatial distribution of O. nigripes was highest in Quadrant C, the most open vegetatively of Plot I and also Quadrants C, D, dominated by P. quadrifarium, of Hill Plot. Data for Plot I O. rutilans show Quadrant B with the highest density the first summer, but by the second, the main population, like in A. azarae, was shifted to Quadrants A, D where cover was most available. On Hill Plot, Quadrant B maintained the highest density during the first summer, Quadrant A dominating winter and the second summer. Both of these quadrants were the most vegetatively heterogeneous of the four and, mentioned previously, favored by A. azarae as well.

Radii of activity

The average distance moved from the center of activity (radii of activity) was calculated for A. azarae, by sex, age, and study plot for each trapping period (Table 26). The age (subadult, adult) of each individual was established according to its weight at first capture in each season. Radii of activity for each animal during any one season were averaged together to give one value in compiling the table.

If the seasonal average distance moved from the center of activity is examined (Table 27) for the adults, by a three-way analysis of variance (Table 28), significant differences attributable to season, sex, and plot were all very significant ($p<.0005$). A season x sex interaction was not significant ($.10>p>.05$).

Observance of Hill Plot A. azarae seasonal radii of activity patterns strongly suggest that winter movements were slightly more than those of summer. In Plot I these mice steadily increased their radii of

Table 26. Average distance, in meters, from the center of activity, with N, for *Akodon azarae*. Data grouped by sex, age class, and study plot for each trapping period.

	Subadult Males				Subadult Females				Adult Males				Adult Females			
	Plot I		Hill Plot		Plot I		Hill Plot		Plot I		Hill Plot		Plot I		Hill Plot	
TRAP PERIOD	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$	N	$\bar{X}$
1 Dec. 1968	1	0.0							2	11.3			4	1.3		
2 " "	3	9.2			3	0.0			9	7.9			11	1.6		
3 Jan. 1969	4	8.0			5	6.2			12	9.7			29	4.1		
4 " "	4	8.8			8	3.2			7	12.7			20	3.6		
5 " "	6	6.4			3	3.8			4	9.3			16	3.3		
6 Feb. "	6	3.3			3	4.0			18	6.6			23	3.3		
7 " "	2	2.7	7	1.6	1	0.0	2	0.0	23	5.7	8	7.1	16	3.6	3	9.1
8 Mar. "	3	4.5	8	6.3	5	2.4	8	4.4	23	4.6	19	8.9	18	5.8	8	8.5
9 " "	2	3.0	3	11.7	4	4.5	1	12.0	19	4.9	23	6.6	14	4.9	5	4.1
10 Apr. "	2	9.0	4	5.5	3	4.0	1	5.3	23	3.8	19	5.8	22	3.9	13	5.7
11 " "	1	8.5	2	5.2	2	11.0	5	8.2	34	5.4	23	5.6	20	3.9	20	6.4
12 May "			1	8.5	4	5.0	4	10.0	21	4.0	30	9.8	14	6.8	18	7.4
13 " "			1	0.0			4	10.2	11	6.6	25	6.6	8	7.2	18	10.6
14 June "			1	16.0	1	0.0			21	7.2	37	8.3	21	5.1	34	8.0
15 " "			2	13.5	1	6.0			21	8.1	26	9.3	20	7.3	22	10.7
16 July "							4	6.9	12	7.2	24	7.0	9	4.2	20	8.0
17 " "	2	6.9	2	3.8	1	5.3	2	9.0	19	6.9	40	9.4	11	7.5	23	8.8
18 " "					2	8.7			23	5.1	23	6.6	25	5.0	15	6.9
19 Aug. "			1	0.0	2	6.0	5	11.9	19	6.6	39	9.1	22	5.0	18	7.7
20 " "			1	12.3	1	42.4			18	6.5	20	8.6	29	5.3	13	10.4
21 Sept. "									15	6.7	14	14.3	13	7.8	9	7.0
22 " "					2	6.0			29	6.5	31	9.2	12	5.4	22	7.7
23 Oct. "					3	4.0	3	7.0	34	9.6	31	8.4	17	7.0	22	8.1
24 " "							1	24.7	28	10.0	23	8.5	20	5.7	17	5.6
25 Nov. "									20	7.3	16	7.7	18	6.5	9	8.6
26 " "									22	10.9	10	10.2	15	7.2	9	12.5
27 Dec. "									16	11.1	2	16.2	21	8.6	3	3.8
28 " "					2	25.6			13	9.6	2	8.7	14	8.3	3	16.6
29 Jan. 1970	1	12.0			1	0.0			8	8.1			6	10.3	1	0.0
30 " "	1	10.4	1	0.0	1	13.4			7	10.8			6	10.6	1	13.4
31 " "	1	8.5	1	6.0	3	6.0			8	11.6	2	6.9	14	14.2	3	6.8
32 Feb. "									6	9.5	2	19.4	5	9.7	6	3.4
33 " "			3	2.0	1	0.0	1	8.5	12	10.6	5	5.6	11	8.0	4	13.6
34 Mar. "			1	8.5	2	6.0			16	7.0	8	2.6	16	5.2	6	7.8
35 " "	1	6.0	1	0.0	2	3.0	1	0.0	13	8.3	7	7.1	13	7.2	4	4.3
36 Apr. "			1	0.0	1	0.0	3	6.8	22	6.2	11	5.7	18	6.4	5	6.8

Table 27. Seasonal average distance, in meters, moved from the center of activity, with *N*, for *Akodon azarae*, by sex, age class, and study plot.

	Subadult Males		Subadult Females		Adult Males		Adult Females	
	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot
First Summer Periods 1-10	4.99 (39)	5.09 (27)	3.96 (49)	2.92 (18)	6.22 (67)	7.60 (36)	3.42 (73)	7.07 (16)
Winter Periods 11-24	7.67 (2)	7.40 (8)	6.61 (10)	9.22 (20)	6.78 (120)	8.87 (100)	5.69 (92)	8.39 (69)
2nd Summer Periods 25-34	9.99 (8)	3.64 (12)	7.72 (10)	6.02 (10)	8.71 (57)	6.90 (38)	7.24 (49)	8.23 (25)

Table 28. Three-way analysis of variance for Table 27 adults.

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square	F Ratio	P
A (season)	600.6200	2	300.3100	13.9037	p<.0001
B (sex)	277.2361	1	277.2361	12.8354	p<.0004
C (plot)	472.6985	1	472.6985	21.8849	p<.0001
A x B (interaction)	106.1216	2	53.0608	2.4566	p<.0865
Within cell		730			

Table 29. Seasonal average distance, in meters, moved from the center of activity, with N, for *Oryzomys nigripes* and *Oxymycteris rutilans*, by sex and study plot.

	Oryzomys nigripes				*Oxymycteris rutilans*			
	Males		Females		Males		Females	
	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot	Plot I	Hill Plot
First Summer (Periods 1-10)	16.67 (2)	20.15 (4)	-	-	36.07 (3)	20.77 (3)	35.65 (3)	25.24 (4)
Winter (Periods 11-24)	11.22 (36)	14.93 (17)	11.35 (19)	15.98 (6)	15.66 (3)	19.93 (9)	10.68 (3)	15.79 (13)
Second Summer (Periods 25-34)	30.00 (1)	6.00 (1)	-	-	17.46 (5)	16.24 (4)	13.64 (9)	13.29 (8)

activity as the study progressed. This is not principally a function of seasonal changes *per se*, but due to the steadily declining habitat quality. The guinea pigs (*Cavia*) are believed responsible for this degradation of habitat, and a further discussion of this follows later. Differences according to sex indicate that males generally have slightly longer radii of activity than females. When the intensity of breeding is high, as in Plot I and to a lesser extent Hill Plot, the first summer females moved lesser distances than in the second summer characterized by low breeding activity. Plot effects, mentioned partially in reference to the influence of *Cavia*, indicate that Plot I animals probably had smaller radii of activity than those from Hill Plot. However, by the second summer, Plot I *A. azarae* had nearly equal or larger radii of activity.

Oryzomys nigripes and *O. rutilans* showed that the average distance moved from the center of activity was 2-4 times more than *A. azarae* (Table 29). The sparse data suggested little else in comparisons made between seasons, sexes, and plots.

Dispersal of *Akodon azarae*

Dispersal, that is, those movements away from the main trapping area, can be estimated for the population in several ways in order to better understand a species' dispersal pattern. Here, the dispersal pattern was determined by trapping other study areas in close association to the main trapping plot. Removal Plot I and II are utilized in exactly this manner to investigate dispersal patterns in *A. azarae*. However, due to the toe clipping scheme used and the fact that Removal Plot I and II have not been analyzed as yet, *O. nigripes* and *O. rutilans* data remain untabulated.

One parameter of dispersal which may be examined is sex ratio; that is, does a certain age class or sex disperse during a given time (winter, summer) at a rate much higher or lower than expected? In fact, this type of examination has already been completed for all three species earlier, when the study area populations were divided into resident and recruit segments (Table 11, 12). The recruits, referring to those captured during the non-breeding months, when recruitment through reproduction no longer is a factor, are dispersers into a given area, and can be examined in this light, even though we have no idea of the distance they have moved in order to enter the study plots. An examination of the above tables and the discussion connected with them should suffice for the moment.

The sex ratios of A. azarae from Plot I and others unmarked from the non-plot areas of Crovetto Pasture, and which dispersed into Removal Plot I and II were also calculated (Table 30). Plot I adults infrequently entered the completed Removal Plot I exclosure during the first several months of trapping because of their relatively low density and the effectiveness of the exclosure. During their increase the guinea pigs (Cavia) likewise became increasingly more numerous, and in addition, destructive on the exclosure. At first the few marked mice captured in Removal Plot I were placed on the nearest Plot I side of the exclosure with the assumption that these mice were including parts of both plots in their home range. However, it soon became apparent that some of these marked mice were dispersing onto the removal plots and establishing a home range. The decision to keep placing marked individuals in Plot I was based on the premise that if they generally resided in a nearby portion of the Plot I, they would tend to remain; if not,

Table 30. Proportion of female *Akodon azarae* of various age classes, seasons, and trapping areas found in Crovetto Pasture. Female sample sizes (in parentheses), and probabilities for null hypotheses of 1:1 sex ratios are also given.

	REMOVAL PLOT I			REMOVAL PLOT II			PLOTS POOLED		
	Juv. SA	Plot I Adults	Crovetto Adults	Juv. SA	Plot I Adults	Crovetto Adults	Juv. SA	Plot I Adults	Crovetto Adults
Winter Per. 11-24	.615 (16) $p>.10$	.308 (16) $.01>p>.005$	.455 (81) $p>.10$	.737 (14) $.05>p>.025$	.263 (5) $.05>p>.025$	.500 (138) $p=1.00$	.667 (30) $.05>p>.025$	.296 (21) $p<.005$	.482 (219) $p>.10$
Summer Per. 25-34	.640 (16) $p>.10$	.429 (3) $p>.50$	.176 (6) $p<.005$	.455 (10) $p>.50$	* -	.378 (17) $p>.10$	.553 (26) $p>.10$	.500 (5) $p=1.00$	.291 (23) $p<.005$
Pooled Seasons	.637 (32) $.10>p>.05$	.312 (18) $.01>p>.005$	.410 (87) $.01>p>.005$	.576 (19) $p>.10$	.318 (7) $.10>p>.05$	.483 (155) $p>.50$	.609 (56) $p>.10$	.321 (26) $p<.005$	.454 (242) $.05>p>.025$

*Only three individuals.

then their subsequent movements would give an indication of their homing ability. Those which repeatedly entered each removal Plot were counted only once in that plot to arrive at the sex ratio calculations. Unmarked adult individuals which entered the removal plots from other parts of the Crovetto Pasture were removed and the data recorded under "Crovetto Adults".

The sex ratio (Table 30) results for the juvenile and subadult group indicate that females, like in Table II, tended to enter the removal plots in slightly higher proportions than males. Toe-clipped juveniles and subadults from Plot I were not captured (one exception) in either of the removal plots. The pooled winter results for "Plot I Adults" suggest that significantly more males than females were entering the removal plots which is in agreement with the winter Plot I resident data. It would be expected that winter "Plot I Adults", like the Plot I recruits are in effect recruits of the removal plots, and should not show any significant differences. This was true for winter "Crovetto Adults", where the results show no significant difference from the expected 1:1 sex ratio, which agrees with Plot I recruit and earlier snap-trap data (Table II). Whether the "Plot I Adults" difference is related to the smaller sample size, the fact that females are slightly smaller than males, so become part of the predominately female subadult group, or some other factor is not known. The pooled summer results for "Plot I Adults" mean little due to the small sample size, while the "Crovetto Adults" show significantly fewer females than expected, a result which agrees with the breeding season (summer) Plot I recruit data (Table II).

During the period in which one or both of the removal plots were

Table 31. Dispersal of *Akodon azarae* from Plot I, calculated as the nearest distance in meters to Plot I - Removal Plot exclosure wall, at the time of first capture away from Plot I. Numbers not in parentheses are those for males; in parentheses, females. The percent of the total which are in each distance category is also given.

NEAREST DISTANCE IN METERS TO EXCLOSURE WALL

	6	18	30	42	54	66	78	90	102	114	126	138	150	162	174	186	198	210
ANIMALS	12(9)	9(2)	6(2)	5(3)	2(1)	1(1)	1(0)	2(1)	2(0)	---	0(1)	0(1)	1(0)	2(2)	---	---	1(1)	3(1)
% OF TOTAL	29.2	15.3	11.1	11.1	4.2	2.8	1.4	4.2	2.8	---	1.4	1.4	1.4	5.6	---	---	2.8	5.6

Table 32. Dispersal of *Akodon azarae* from Plot I, calculated as the nearest distance, in meters, from the point of last capture in Plot I to the first point of capture within Removal Plots I and II. Numbers not in parentheses are those for males; in parentheses, females. The percent of the total which are in each distance category is also given.

NEAREST DISTANCE IN METERS TO POINT OF LAST CAPTURE IN PLOT I

	0-18	18-36	36-54	54-72	72-90	90-108	108-126	126-144	144-162	162-180	180-198	198-216	216-234	234-242	242-260	260-278	278-296	296-314
ANIMALS	5(6)	14(1)	2(2)	3(1)	2(1)	4(2)	2(0)	1(1)	1(1)	0(0)	0(0)	2(2)	0(1)	0(0)	1(0)	1(0)	1(1)	1(0)
% OF TOTAL	18.6	25.4	6.8	6.8	5.1	10.2	3.4	3.4	3.4	---	---	6.8	1.7	---	1.7	1.7	3.4	1.7

in operation, approximately 469 _A. azarae_ were present at one time or another in Plot I. About 72 of them, or 15.4 percent, eventually appeared in the removal plots. The dispersal of these individuals from Plot I, calculated as the nearest distance, in meters, from the Plot I-Removal Plot exclosure wall to the first point of capture in either of the removal plots is given in Table 31. Following that, Table 31 gives dispersal distances from the point of last capture in Plot I to the first point of capture within either of the removal plots. In either case, nearly 45 percent of the dispersers moved relatively little, _i.e._, only 6-18 m in Table 30, or 0-36 m as calculated in Table 32.

These same individuals, if summed at the trapping period at which they were first captured in the removal plots, then divided by the Plot I minimum number known alive for the time during which the animals dispersed (Table 33) show no definite dispersal rate patterns. The May rate, calculated for Removal Plot I individuals only, is rather high and suggests a causal relationship with a substantial rainfall that left several inches of standing water on the Crovetto Pasture for nearly a week. July and especially August rates likewise might reflect late winter suboptimal conditions for _A. azarae_. New vegetational growth began to slowly appear in September.

Homing of Akodon azarae

Homing ability for _A. azarae_ very quickly became an area of interest during the removal studies because of the large number of Plot I mice trapped and removed, only to have them return the next day or two to or near the same trap of original capture. Homing was defined as the return of an animal during the same four day removal plot trapping period to the same trap where it had been captured or at another

Table 33. The monthly rate of dispersal, in percent, for Plot I Akodon azarae, based on the number dispersing to Removal Plot I and II, and the minimum number known alive in Plot I at the beginning of each new month of dispersal.

	MONTH AND TRAPPING PERIOD											
	Apr. 11	May 13	June 15	July 17	Aug. 19	Sept. 21	Sept. 22	Oct. 24	Nov. 26	Dec. 28	Jan. 30	Feb. 33
% DISPERSERS	1.9*	6.5*	4.5	6.2	10.8	3.1	1.1	8.2	3.8	7.7	2.1	3.6
NO. DISPERSED	4	12	8	10	15	4	1	8	3	4	1	2
MIN. NO., PLOT I	214	185	179	162	139	127	94	97	78	52	47	55

*Only includes Removal Plot I.

Table 34. Homing success at various distances for Akodon azarae with: (A) giving the number of animals which had at least one opportunity to home, (B) the number which actually did home, and (D) the number of times homing took place for (B) individuals. Data were tabulated for each trapping period, then summed over all periods to present this compilation.

	HOMING DISTANCE IN METERS																	
	6	18	30	42	54	66	78	90	102	114	126	138	150	162	174	186	198	210
(A) NO. ANIMALS	34	32	26	14	11	12	10	10	16	14	8	4	5	7	3	5	10	12
(B) NO. WHICH HOMED	15	15	12	6	3	7	6	4	7	3	3	3	1	1	1	1	5	8
(C) % WHICH HOMED	44.1	46.9	46.2	42.9	27.3	58.3	60.0	40.0	43.8	21.4	37.5	75.0	20.0	14.3	33.3	20.0	50.0	75.0
(D) NO. TIMES HOMED	25	23	16	10	7	9	10	7	7	3	5	4	1	1	1	3	9	10
(E) RATIO OF $\frac{D}{B}$	1.67	1.53	1.33	1.67	2.33	1.29	1.67	1.75	1.00	1.00	1.67	1.33	1.00	1.00	1.00	3.00	1.80	1.25

trap station adjacent to it. This allowed the mouse to be captured again in a possible nine traps, none more than 17 m from the original. If an Akodon was recaptured, this station then served as a new center for possible successive captures. The fourth day was only examined to determine if earlier animals had homed.

This method should give minimum values for homing ability for three reasons. First, animals for the first three days of each trapping period were tabulated. By so doing, animals captured the second and third days did not have equal time to home as the first day. Second, some animals were not perceived to "home" until subsequent three day trapping periods. Third, mice could be recaptured adjacent to the homing area, and although it was suspected from their movements, past and present, that they were in their home range, these mice could not be considered. Since sexual differences do not seem to exist for the short distances involved here (Fisler, 1962; Furrer, 1973; Robinson and Falls, 1965), sexes were pooled.

Homing success at various distances (Table 34) for A. azarae for the four day trapping periods indicate that an average 42.0 percent of the individuals home, regardless of distance. In addition, the ratio of the number of times an individual homes over the number of individuals shows little difference (perhaps a smaller ratio) with distance.

Habitat Quality

Influence of Cavia on Akodon populations

Plot III (Figure 2) was established in late spring (December, 1969) when it was clear that the Cavia aperea population had reached substantial numbers in the Crovetto Field, and was in some way depressing Akodon and Oryzomys numbers, and probably the other rodent species as well.

It was hypothesized that *Cavia*, through their devastation of vegetational cover, were negatively affecting *Akodon* density. Although *Akodon* is the principle myomorph grass-eater, food is really no problem since *Cavia* graze on higher parts of the vegetation. However, *Cavia* do consume the inflorescences, so whatever part seeds contribute to the *Akodon* diet was presumeably lost. *Akodon* and *Cavia* were found together in Sherman traps at least a dozen times in the course of the study and at no time did the guinea pig show any sign of predation upon *Akodon*, nor are there any recorded instances of them so doing.

Except for December when the nine Sherman traps were set in Plot III for five days, the months January-April each had four-day trapping periods. Five larger box traps were examined daily for *Cavia* which may have entered the plot during the months of December to 25 March 1970. By the end of March, *Cavia* were entering Plot III in large numbers. From 25 March - 19 April 1970, one dozen Victor-Oneida No. 0 steel traps were also placed within the plot to reduce the number of *Cavia*. During this period, traps were checked at least once a day and often twice.

Although trapping in this manner is going to bias upwards any attempt to give true values of *Cavia* densities outside Plot III, some figures are necessary. From this 36 m x 36 m (.13 hectares) plot, 45 guinea pigs were removed from 1 December - 25 March, a period of 115 days. After that to 19 April (25 days), 65 *Cavia* were captured. On 15 March and 15 April, two *Lutreolina*, one each day, were live-trapped and released where captured. One hurón, *Galictis cuja*, likewise was taken on 31 March. Of 22 adult *Cavia* females examined during the period from 1-19 April, 39 young were found in 21 animals, an average

Figure 14. Removal Plot I adjacent to Plot III - Removal Plot I exclosure. Note the cane on the ground, the lack of inflorescences, and the generally grazed appearance of each grass (Paspalum elongatum) clump.

Figure 15. Same position and date as that for Figure 14, but with a turn of 180°, and now looking into Plot III. There is somewhat less cane on the ground, the inflorescences are abundant, and the grass clumps are much denser and less disturbed.

Figure 14

Figure 15

of 1.9 (mode of one) per female. Rood (1972) found a mean litter size of 2.1 for this species.

The *Akodon* population during this five month period was as follows: 4, 3, 7, 14, and 16, the latter figure nearly equal to the densest quadrant population of *A. azarae* found in Plot I during the corresponding time, Quadrant A (25 traps, .36 hectares, versus 9 traps, .13 hectares for Plot III).

One *Akodon* female was recorded pregnant in December and two others contributed a total of 7-8 young in February and also in March. A population of 14-16 may have been near the upper limit for Plot III since 11 of 14 or nearly 80% of the March *Akodon* were not present in April. Their disappearance could also be due in part by predation as well as emigration, the latter facilitated by exclosure disturbance as *Cavia* attempted to jump over or dig under the metal sheeting during repeated attempts to enter or exit.

DISCUSSION

The first objective of this study was to compare and contrast the various demographic and ecological changes which occur in a yearly cycle of grassland-inhabiting South American (Argentine) myomorph rodent populations, namely the grass-eater, *A. azarae*, the peromyscine-like, seed-eating rice rat, *O. nigripes*, and lastly, the insect-eating *O. rutilans*. This objective was only partly realized in the latter two species because for the sake of larger sample sizes, their two field populations were often pooled. Whenever possible, however, the two field populations were compared and where pertinent, these results are summarized. The main objective, however, was to compare and contrast the basic demographic and related ecological and behavioral features of the South American pampan species with the North American temperate grassland myomorphs. Before this discussion commences a brief commentary concerning the origin and evolution of the aforementioned species follows.

Phylogenetic History of *Akodon*, *Oryzomys*, and *Oxymycteris*

The tribe Sigmodontini (subfamily Cricetinae, family Muridae), to which *Akodon*, *Oryzomys*, *Oxymycteris* and a number of other genera belong, is the most primitive and diversified of New World murids (Hershkovitz, 1972). The adaptive radiation of the Neotropical Sigmodontini led to a group consisting of some 40 genera and 150-200 species (Hershkovitz, 1972), which presently occupy arboreal, pastoral, palustrine, and aquatic habitats and have equally variable food habits.

The origin of Sigmodontini is questionable. Hershkovitz (1969) and

Patterson and Pascual (1972) supposed that they originated in boreal America, then spread into Eurasia and South America. However, Hershkovitz (1972) pointed out that there is no evidence that South American sigmodontines existed in boreal America prior to their invasion to the former in the late Pliocene. He felt there is no likelihood that they gave rise to, or were descended from Eurasian cricetines. Whereas earlier, Hershkovitz (1962) attributed similarities between sigmodontines and African (and Malagasy) cricetines as products of parallelism, he now speculates (Hershkovitz, 1972) that it is likely that ancestral sigmodontine stock were rafted from Africa to South America during the early Tertiary.

Cytogenetic work by Bianchi *et al.* (1971) suggests to them that the akodonts, a progressive offshoot of the Sigmodontini, must have radiated from the central Andean region bounded by southeastern Peru, northern Chile, Bolivia, and northwestern Argentina. They give no date for these events but Reig and Linares (1969) list an already specialized pastoral *Akodon* from Argentina as one of the oldest (late Pliocene) known sigmodontines. Oxymycterines are described by Hershkovitz (1972) as being long-clawed, shrew-like, semi-palustrine, insectivorous mice with akodont antecedents. In the oryzomine stock, the small mice of the scansorial subgenus *Oligoryzomys*, of which *O. nigripes* is a member, did eventually invade grasslands, but according to Hershkovitz, not until the Pleistocene.

The North and Central American distributed Peromyscini, including such insect- and seed-eating genera as *Baiomys*, *Peromyscus*, and *Reithrodontomys*, is regarded by Hershkovitz (1972) as derived from isolated offshoots of Eurasian cricetines; they are known from the

Oligocene. The typically boreal grass-eating Microtini, which with the peromycines are continuously referred to in this manuscript, represent a late-appearing cricetid tribe known first from the late Miocene (the period of vast grassland development) of North America, and the Pliocene of Eurasia (Dawson, 1967).

Population Changes

Seasonal density changes

The *A. azarae* population of Plot I literally exploded during the summer preceding the *Cavia* invasion and remained high (greatly so from about February to June, 1969) throughout the duration of the study. By the second summer *A. azarae* reached only one-third to one-half of its first summer's density. This reduction appeared due to the devastation of cover by *Cavia*. The Hill Plot *A. azarae*, on the other hand, showed approximately the same population densities for those parts of both summers on which data were collected, though somewhat lower the second breeding season. In contrast to Plot I, hardly any guinea pig activity was noted on the Hill Plot during this study.

The Plot I *O. nigripes* similarly had a high population during the first portion of the 1969 winter, probably in response to a good seed crop (a result of ample rain?) from *Paspalum elongatum* that first summer. None was ever recorded from Plot I after period 25. Very likely the *Cavia* were responsible for this drastic decline of *O. nigripes* as nearly all infloresences were consumed before their maturity the second summer. Only *O. rutilans*, possibly because of its mainly insectivorous habits appeared to escape the drop in density experienced by the former two species.

Irruptions and cyclic flucuations

The high density populations observed for *A. azarae* in Plot I and Hill Plot during the first summer of study may be an example of an irruptive event for the species. Crespo (1966) discusses other irruptive peaks which were documented in Buenos Aires Province for *A. azarae* and several other species in 1833, 1872-73, 1944, 1963 and 1964. Crespo (1944) found that irruptions, at least during some years, were correlated with periods of abnormally high summer rainfall. If, after more intensive investigations this proves to be the case, then the high density evidenced the summer-fall of 1969-70 could be attributed to that year's increased precipitation (160 mm over the normal). Irruptions of other grass-eating cricetines, such as the North American species of *Sigmodon* and *Oryzomys*, appear to be irregular in period and mainly influenced by climatic factors (Erickson, 1949; Fleharty et al., 1972; Goertz, 1964; Negus et al., 1961). In agreement with Pearson (1967), there is no evidence of rhythmical cyclic fluctuations in *Akodon* similar in nature to those found for many Northern Hemisphere microtines (Chitty 1960, 1967; Krebs, 1964, 1966, 1972; Krebs et al., 1969).

Density estimates and seasonal variations

Density estimates for many grass-eating microtines at various localities and population levels were summarized by Aumann (1965). More recent density estimates are given by Krebs (1964, 1966), and Krebs *et al.* (1969). Estimates for *Sigmodon* (Goertz, 1964; Howard, 1955; Petersen, 1973) and *Oryzomys palustris* (Negus *et al.*, 1961) are within the same order of magnitude. For seed-eaters, Terman (1966, 1968) gives compiled data for a number of different rodents, including species of *Peromyscus*. The results suggest that *Peromyscus* population levels are typically low. In addition, these populations exhibit, on the average, smaller seasonal mean variations than the grass-eating microtines. Terman's limited data for the seed-eating *Reithrodontomys megalotis* mean variations appear to fall closest to that of the microtines. Insectivorous mice of the genus *Onychomys*, based on their relative density to other species captured the same time (Egoscue, 1960) inhabit areas at even lower densities than the seed-eaters.

In summarization, evidence is given to indicate that *A. azarae* reaches densities usually reported for microtines and other grass-eaters, and that *O. nigripes* is similar in population levels and variation to North American seed-eaters. *Oxymycteris rutilans* is somewhat similar to the insect-eating *Onychomys*. Information provided by Egoscue (1960) suggests that this is true. Terman's (1966, 1968) compilation of NACSM information on the shrew *Blarina brevicauda* also is in agreement with this pattern.

Trappability

Krebs *et al*. (1969) found that *Microtus ochrogaster* was very trappable (90%) while *M. pennsylvanicus* was less so (50-80%). Additionally, *M. pennsylvanicus* was less trappable during the summer than at other seasons of the year. *Akodon azarae* was most similar to *M. pennsylvanicus* in overall trappability as well as summer trapping success. However, Krebs *et al*. achieved their success in only two consecutive nights of trapping whereas here it was three.

Trappability of *O. nigripes* and *O. rutilans* varied considerably within and between plots. In general, their trappability was less than that found for *A. azarae*. The only exception was Hill Plot *O. rutilans*, where the results are comparable to those for *A. azarae*. Trappability data for North American seed- and insect-eating rodents are sadly lacking.

Trappability may differ between sex and age classes within a population. Smith (1968) found slight differences in *Mus musculus* and major differences in *Peromyscus polionotus* trappability, according to sex. Females pregnant and/or lactating were not as likely to be captured. Krebs *et al*. (1969) found little or no difference in their two species of *Microtus*, irrespective of breeding season. With regard to age (weight) classes, Davis and Emlen (1956) found that large (older) Norway rats are trapped sooner than smaller (younger) individuals. Information concerning trappability within a three day trapping period and segregated by species, age, sex, and season will be discussed later under the heading "Movement Patterns".

Adequate sample sizes of all species, plus species specific activity patterns make trappability comparisons difficult to evaluate. Since each species does not have an equal liklihood of entering a trap (perhaps because individuals of another species with an earlier period of activity have filled the traps), the use of different trapping schedules or multiple trap stations should be considered. This is assuming that behavioral differences are not great enough to seriously affect trappability between species.

Recruitment

There appears to be little or no data reported on this demographic parameter for other rodents. Recruitment into a population may come from new animals immigrating to the study area or by recording for the first time animals which were born within the area and have attained trappable age. During the breeding season, these two components have yet to be satisfactorily separated.

For *A. azarae*, the data presented earlier show that recruitment is highest during the summer (breeding) seasons and lowest during the winter. Concerning _O. nigripes_, reproductive activity, as measured by testis and vaginal condition, and embryo palpation, seemed to be too low to account for a major portion of recruitment. Instead, it is believed that recruitment rates remained high because of immigration, particularly in the Crovetto Pasture (Plot I) where the highest densities formed. In fact, a breakdown of recruitment by study plot showed that the _O. nigripes_ recruitment rate in Plot I was approximately double that found for Hill Plot.

Oxymycteris rutilans presents the best example of a change in recruitment pattern due to season. Reproduction occurred at approximately the same rate year-round. Therefore, any great change in recruitment is likely due to a change in emigratory-immigratory patterns. In _O. rutilans_, it appears that there was less vagility in the winter season. Data presented earlier show that the animals tended to restrict themselves to a smaller area during the winter months.

An examination of _O. rutilans_ recruitment patterns show that the drop in winter rate was the result of fewer adults immigrating into the study plots. Recruitment weights show approximately the same percentage (70-75 percent) of adults in the first summer as in the winter. During the second summer, the same number of adults continued to be recruited as during the first. However, a greater number of young animals were also added to the total recruitment list. The result was that only about 30-40 percent of the recruits consisted of adults. The reason for the upsurge in the number of young recruits is unknown. It is known that the number of young recruits amounted to about 20-25 percent of the number of embryos counted by palpation during the first summer and winter. The second summer young recruits accounted for nearly 90 percent of the number of embryos counted that season. Assuming that juvenile mortality is most likely to occur in the season the embryos were counted, and that emigration-immigration rates remained approximately equal, the 90 percent reading indicates a high survival of young compared to the former two seasons. It is interesting to speculate whether earlier high densities of _A. azarae_ during the first summer and winter had affected _O. rutilans_ juvenile and subadult survivalbility.

If the pattern observed for _O. rutilans_ is applicable for _A. azarae_, which similarly showed restricted movements during the winter, then high summer recruitment is a function of higher adult recruitment rates (at least higher than winter adult recruitment), as well as a function of the number of young animals reaching trappable age.

Indeed, when the recruitment segment of the population is divided into adult and young animals by weight in the same manner as that for _O. rutilans_, it was found that adult recruitment in _A. azarae_ for the winter season was only about 7-8 percent of the total number of animals captured each trapping period. When the summer season was examined, the number of adult recruits each period increased 2-4 fold over the winter season percentages.

Since adult recruits may be viewed as dispersers (disperse into the study plots) the winter-summer trends just noted should also be evident in the dispersal rate data determined in the Plot I to Removal Plot I and II _A. azarae_ movements. This is not the case. If anything, the winter (May-August) dispersal rate (which incidently agrees favorably with the adult winter recruitment rate) was slightly higher than the summer rate. There seems to be one likely interpretation of the low summer dispersal rates. Because of the Cavia devastation, Removal Plot I and II were in very poor condition by the second summer. The area on which Plot I was located was the most mesic part of the entire Crovetto Pasture, except for portions around the Arroyo Pantanoso. As a result, it fared best during the summer and offered more cover and food than the rest of the field. By so doing, dispersal away from Plot I might have been reduced, while recruitment (dispersal into the plot) would continue.

Sex Ratios

Neonate A. azarae, as described in Appendix A, did not show any significant departure (1:1.2) from the expected 1:1 sex ratio. The sex ratios observed in the field data demonstrate that females generally form the smallest proportion of each period's catch during the winter (non-breeding season). However, during the breeding season, the females constitute a much higher proportion of the catch, although not necessarily over .500. Crespo (1966) did not find this trend in his snap-trapping study. He reported an excess of males, and unlike here the preponderance was at its greatest during the peak of the reproductive season. These results must be an effect of snap-trapping, since similar snap-trapping results were found in this study (Table II).

Differences in sex ratios were noted in this study between resident and recruit segments of the A. azarae population. This is evident in the "ALL AGES" grouping where resident females make up a significantly smaller proportion in the non-breeding season of both study sites, whereas there is no significant difference within the recruits. In the summer, resident females constituted a greater proportion than they did during the winter season.

One explanation for the recruit-resident sex ratio disparity could be that the resident mice do not enter the traps as often during the non-breeding season. Because it was mainly the resident population which was doing the breeding, not the recruits, high energy demands (two or three fold increase of food intake) during pregnancy and lactation (Kaczmarski, 1966; Nelson and Evans, 1961), and possible increased activity during periods of estrus (Eayers, 1954; Wang, 1923) could increase their susceptibility to live-trapping.

In support of this explanation, reproduction, which was highest during the high density season, also shows the highest proportion of females for the two breeding seasons. Unfortunately, first breeding season data are lacking for Hill Plot.

Krebs *et al*. (1971) found that although laboratory results for *Microtus pennsylvanicus* and *M. ochrogaster* documented 1:1 sex ratios in neonates, field results showed 53-55 percent of the resident trappable animals to be females. Secondly, and in contrast, the sex ratios of newly caught animals (recruits) showed a significant paucity of females (44-46 percent). Their first finding of a high proportion of resident females can perhaps be explained in light of my interpretation of the *A. azarae* sex ratio data. Since *M. pennsylvanicus* and *M. ochrogaster*, like many microtines, breed more or less continuously, Krebs *et al*. could not examine the effect of breeding activity upon sex ratios.

Other studies have demonstrated similar sex ratio results. *Microtus californicus* appeared to follow this trend at Kreb's (1966) Tilden Control Plot, and Getz (1960) found *M. pennsylvanicus* in Michigan to do the same. Crawley (1969) also presented the same type of sex ratio results for *Clethrionomys glareolus* and *Apodemus sylvaticus* of England. However, not all field studies show the above trend. Goertz (1965a,b) stated that when the *Sigmodon hispidus* population density was highest but with little breeding, there were slightly more females than males. During times of low density but more intensive breeding, significantly more males than females were trapped.

Unfortunately, it is difficult to determine if female *A. azarae* are more susceptible to live-trapping during the breeding season than during the non-breeding season. One method of arriving at an answer would be to examine "trappability" between the sexes, which has yet to be done. One reason for not pursuing this analysis was based on the work of Krebs *et al*. (1971). Of several *Microtus pennsylvanicus* and *M. ochrogaster* populations studied, in only one population (*M. pennsylvanicus*) was there a significant difference between the trappability of the two sexes. The authors concluded that differential trappability of males and females was rare, and therefore of lesser importance than other factors effecting sex ratios (*e.g.*, differential secondary sex ratios, recruitment, growth, movements, and survivalbility).

Another approach is to find whether the captures per animal within each three-day trapping period vary by sex and season. If females are captured more times per trapping period during the reproductive season, then intuitively there is a greater liklihood that a larger percentage of the total female population will be captured.

Akodon azarae recapture data, analyzed within each three-day trapping period, support the above reasoning. Trappable adult females for the high density summer season of Plot I were captured at an average rate 10 percent higher than males for the first seven trapping periods when breeding levels were highest (Table 21). Results for the first ten trapping periods (Table 23), which includes the decline of breeding also shows this trend for Plot I and Hill Plot, but not quite as strongly. Winter recaptures were nearly equal in both sexes for both plots. Plot I second summer season results, when breeding was less intense, show overall recaptures up (less density, so less competition for traps?) from the first season, with males slightly more than females. Hill Plot results for the second breeding season show females to be 9 percent more susceptible to capture than males. This could be a reflection of the higher intensity of breeding (Table 13) compared to Plot I.

Only one study was found that examined captures per animal. Gentry (1968) studied pine mice, Microtus pinetorum, in two enclosed field plots. His results pointed out that females were captured less often than males during the summer but not during the winter. This is just the contrary of the above results, but may be due to the fossorial habits of this species.

In reference to the second finding by Krebs et al. (1971), that female recruits represent a smaller proportion of the sex ratio than the residents, the A. azarae data are also in general agreement. As discussed earlier, it is the proportion of resident females during the breeding seasons which are significantly higher. The recruit females (fewer reproductive animals?) are not significantly different from the expected 1:1 ratio. During the non-breeding season, however, the resident females drop significantly lower than .500, and the recruits remain relatively unchanged. The difference in the two segments of the female population, particularly during the non-breeding season, must be a measure of the intensity of selection on recruit populations to arrive at resident sex ratios. In summer (breeding) populations, behavioral mechanisms tied into the reproductive cycle appear to be a driving force in effecting the difference in the proportion of resident females captured.

Oryzomys nigripes populations were found in this study and by Crespo (1966) to have an excess of males. Information compiled by Terman (1968) for the seed-eaters of the genus *Peromyscus* indicates that this seems to be the case with them also. Dunaway (1968) found just the opposite for *Reithrodontomys humulis*, although closer examination of his data suggest that the preponderance of females were normally captured during the breeding season, and that non-breeding populations were nearer a 1:1 sex ratio, or even slightly favored males. Few of the *O. nigripes* were discerned to be pregnant, particularly on Plot I, so this non-breeding population would be more inclined to lean towards a higher proportion of males.

The *O. rutilans* data, which heavily favor females, regardless of time of year, may in fact be at least partly attributed to the continuous reproductive state of the females. These data then follow the pattern which is apparent in most other closely-studied rodent populations; that is, the females are most prevalent in breeding season trapping records, and less so during the non-breeding portion of the year.

Fisler (1969, 1971), attempted to correlate sex ratios with ecological and social organizational systems in three species of *Reithrodontomys*. He found males were favored during low densities and breeding occurred year round. When breeding was at its highest, the male sex ratio was even higher than during periods of less intensive breeding. The reason for this preponderance of males during the breeding season is unknown.

The consistently higher sex ratio of males to females irrespective of time of year, is thought by Fisler to be an adaptive feature for these low density, small, secretive mice where the number of young-bearing females are at a premium. The reproductive strategy in such a case is to have many reproductively-active males moving about to assure insemination of any females that come into estrus, rather than assuming that one male may contact several females, as is probably the case in most high density species where social contact is not a critical problem.

Reproduction

Details of the post-natal development and sexual maturation of young *A. azarae*, *O. nigripes*, and *O. rutilans*, including a comparative examination of them in relation to their North American counterparts, are discussed in Appendix A.

The length of the breeding season differs for each of the three Argentine species. The Uruguayan (33^{o}-35^{o}S) *A. azarae* bred from October through May (Barlow, 1969). In addition, Barlow mentioned the discovery of one pregnant individual collected in the southern part of the country in September, 1957. In Argentina, Crespo *et al.* (1970) observed pregnant *A. azarae* in southern Cordoba 33^{o} 50' - 34^{o} 35'S) from October to May. In the northern part of Buenos Aires Province (34^{o} 15'S), Crespo (1966) has trapped pregnant animals from October to March. Pearson (1967), who captured *A. azarae* near the city of Buenos Aires (35^{o}S), found the season of births to extend from October to April. Further to the south (37^{o} 45'S), the Balcarce populations were found to have a somewhat shorter breeding season, extending from the first week of November to the middle of March or April, depending on the site.

These data point out that *A. azarae* has a definite 5-7 month breeding season during which it is able to reach and maintain high densities (instantaneous rates of population growth to r=.13, very comparable to those of some microtines, according to Krebs *et al.*, 1973). During the period of high density growth, *A. azarae* seemed to have a slightly extended breeding season. Winter breeding is a common occurrence in microtines (Krebs, 1964, 1966; Krebs *et al.*, 1969), and *Sigmodon* (Goertz, 1965) and *Oryzomys* (Negus *et al.*, 1961) in the southernmost parts of their U.S. range.

Observations by Crespo (1966), Pearson (1967) and from the present study show that young of the year do participate in reproduction during the same season in which they are born. My field data indicate the young commence breeding when approximately two months of age. However, it appears that young do not become reproductively active if they have not reached two months of age (about 18-20 g) by the last days of February or first days of March.

In agreement with the findings generally reported for microtines (Hamilton, 1937a; Keller and Krebs, 1970; Krebs *et al.*, 1973), *A. azarae* attained sexual activity at a lower age during the period of high density growth (first summer, see Tables 16, 17). Secondly, litter sizes were the same regardless of the population density. This last feature may or may not occur in microtine populations at high densities (Schaffer and Tamarin, 1973). Concerning other grass-eating species, Odum (1955) found that *Sigmodon hispidus* litter sizes were greater in years of high density than those from years of low density. Negus *et al.* (1961) found the same occurrence in *Cryzomys palustris*. Negus *et al.* noted that younger animals reached sexual maturity at this time also. It appears that the features just mentioned are shared to one extent or another by many rodent species and serve as mechanisms to increase productivity during favorable conditions.

Shifting the discussion to *O. nigripes*, Barlow (1969) believed that April and May were the months of peak reproduction, and the earliest active female was found lactating in January. Crespo (1966) maintained that *O. nigripes* reproduced during the same months as *A. azarae*; that is, from October to April. The Balcarce animals were at such low densities during the early summer of both seasons that it is difficult to set a date for the initiation of reproduction. Scrotal animals were first detected in the last week of November. No embryos were palpated in the few females present until January. Breeding continued into May, possibly longer (August?).

This study, like Barlow's, suggests that *O. nigripes* probably breeds later into the autumn than *A. azarae*. The period of peak reproduction could not be discerned in this study, although a good proportion of the population was reproductively active in February and March. No females were captured more than once. This may be due in part to trap mortality and a higher dilution rate. Since several female *O. nigripes* weighing 16 g (about three months of age) in January were or shortly after became pregnant, it appears that young born early in the reproductive season do become sexually mature the same season.

However, whether early young of the year do reproduce during the same reproductive season can be questioned. One of the young animals referred to in the above paragraph, first captured the first week of January at 16 g took nearly two months to gain 5 g (it was detected to be pregnant at its second capture). If the laboratory postnatal growth data approximated growth rates under field conditions, then it takes approximately three months of age to reach 10-12 g, and since growth is already reduced by that time, it would take at least another two months to reach 16 g. This would make the animal about five months of age by January, with a birth date around the first of August or earlier if winter growth is retarded in this species. The latter possibility may be true since scrotal (=breeding) males were not found after May, and 13 g animals were still captured as late as September. Crespo (1966) also reported low weights for young mice in late winter.

Reproductive data for seed-eaters, primarily *Peromyscus*, are scanty (Terman, 1968) and not readily comparable in many aspects with the similarly poor *O. nigripes* information. Howard (1949) found that prairie deermice (*P. maniculatus bairdi*) formed a bimodal distribution of births, with a peak in late spring produced by overwintering adults, and a higher peak in the fall produced by young born earlier in the year. The same trend appeared in the eastern harvest mouse (Dunaway, 1968). It is suspected to occur in *O. nigripes*. There may also be a similar synchronization of breeding in *A. azarae* (Table 13). Overwintering adults produce a peak of young in the spring. A few old adults and their first litter continue for one or at most, two litters more before their young began to breed just as fall arrives.

Year-round breeding of *O. rutilans* was suspected by Barlow (1969), and documented here. His sample of the other Uruguayan insectivorous myomorph, *Scapteromys tumidus*, showed that this animal also appeared to breed year-round. Perhaps insectivorous rodents, in a given set of climatic conditions, have a more stable year-round food supply than do grass- and seed-eaters.

In areas where food supplies dwindle during the much cooler winter (unlike the less harsh climes of Uruguay and Balcarce, Argentina), continuous breeding may not be possible for insect-eaters. Winter breeding has not been reported for the North American _Onychomys_ (Egoscue, 1960; Horner and Taylor, 1968), presumeably because of the paucity of proper foodstuffs or perhaps other environmental factors. The best known of the North American shrews, _Blarina brevicauda_, is apparently capable of at least low intensity winter breeding (Dapson, 1968). Winter food habits of _B. brevicauda_ indicate that animal food continues to be of major importance, although vegetation intake approximately doubles in volume (Hamilton, 1930).

Survival Rates

One of the most difficult parameters to calculate for mice is survival. According to past researchers, the survival of a rodent depends on such factors as age, movements, sex class, season, dispersal, recruitment, predation and population phase (Getz, 1960; Krebs, 1966; Krebs _et al._, 1969, 1973). Some of these parameters have been or will be covered in other sections of the discussion. Others are not critical to the point which is to be stressed here; that is, are survival rates of grass-eaters and seed-eaters different?

Unlike Holarctic microtines, _A. azarae_ does not breed in the winter, so any population decline at this season can be mainly attributed to mortality. This assumes that immigration and emigration approximately compensate each other. True survival rates for the trappable population, then, should be closer to 90-95 percent for the winter season than the minimum survival rate of 80-83 percent.

Can the difference between these two values be explained in light of the data analyzed thus far? Dispersal rates for Plot I equalled about

5 percent per month, regardless of season, based on the dispersal data. If the road side of Plot I is considered a formidable barrier to dispersal and something near 5 percent also disperses from the other two sides for which no data are available, a minimum of 15 percent is known to disperse each month, or 7.5 percent between trapping periods. This latter figure approximates the winter recruitment (dispersal into) rate (9 percent). Changes in movement (radii of activity) and adult recruitment, (and presumeably dispersal though not shown here), and the onset of reproduction make it unreliable to obtain summer true survival rates.

The effect of predation on *A. azarae*, as indicated by an analysis of over 300 predatory mammal scats and bird-of-prey pellets collected from the Crovetto Pasture during the duration of this study suggest that predators contributed at most only several percent to the *A. azarae* (and the other two species also) mortality rate per month.

As stated by Krebs *et al*. (1973), death rate measurements are available for a relatively small number of rodent populations. However, it appears that *A. azarae* enjoys a rate roughly comparable to that for microtines (Krebs, 1964, 1966; Krebs *et al*., 1969). *Oxymycteris rutilans* may fit in the category with *A. azarae* and the microtines. Survival values for *O. nigripes* are somewhat below the former two Argentine species. This is not what might be expected since other seed-eaters such as those studies cited by Terman (1968) for *Reithrodontomys humulis* strongly suggest that population turn-over takes longer in these forms as compared to grass-eaters. Perhaps the disappearance of *O. nigripes* from the community is due to emigration from the study sites to other areas with more food resources or is a result of their grouping behavior

(Crespo, 1966), discussed later.

Movements

Much of the information originally covered in the "RESULTS" section concerning movements and dispersal have been discussed under the headings previous to this and will not be thoroughly covered here. Emphasis will be given to as yet undiscussed topics.

The spatial distribution, utilizing the centers of activity, was determined for each species by dividing both Plot I and Hill Plot into four quadrants. For Plot I animals, A. azarae and O. rutilans were densest in those areas where vegetation cover was most dense. As vegetation characteristics changed under the influence of Cavia so did the densities of the above two species shift to take advantage of remaining cover. Oryzomys nigripes was not so restricted to vegetative cover during the first half of the study. The quality of vegetative cover was found by vegetation analysis to be much less in Plot I by the second summer. The Cavia exclosure experiment documents the damage these animals can do to a fallow pasture planted in selected grasses. The effects of the large density build-up of Cavia is reflected in the lower densities (disappearance of O. nigripes) and changes in the spatial distribution of the small rodent inhabitants as they adjusted to the new carrying capacity of the pasture. The Hill Plot species, particularly A. azarae, reflect the heterogeneity of the cover in that the difference from one quadrant to another was much less than in Plot I. This was not expected because of the large percentage of pure Paspalum quadrifarium stands. Apparently this unpalatable grass offers an abundant seed supply in season, as well as abundant cover (including a thick layer of ground debris) for invertebrates and nesting activities.

"Recapture per trapping period" data indicate the probability of recapturing a mouse more than once during any three-day trapping period. Plausible reasons why species differences in recapture were discussed earlier. Within species differences suggested that resident adult *A. azarae* females were recaptured more frequently than males.

Movement data (Table 27) for adult females in the high-density season in Plot I, and to a certain degree Hill Plot, strongly suggest that during seasons of high reproductive intensity, the distances traveled is reduced. Krebs (1966) stated that *Microtus californicus* males averaged longer movements between captures than females during the breeding season, but this was not the case during the non-breeding epoch.

A more correct interpretation, particularly in reference to *A. azarae*, should include the recognition that female mice under high intensity breeding will show markedly decreased movements (and become recaptured more often). Reproductive activity of the females reduces the length of movements between captures more than do different seasons or densities. This reasoning is sensible when one realizes the different energy demands and behavioral patterns associated with the gestation and care of the young. In such periods of reproduction, the females restrict themselves more to foraging near the nest. This behavior presents no food-acquiring problems since food, be it insects, seeds, or grasses, is generally not resource-limited during periods of peak reproduction. A study by Blair (1953) supports my interpretation of the movement data. He found that two species of kangaroo rats in a southern New Mexico mesquite association ranged less widely at about the onset of the reproductive period.

By examining movement data within a trapping period, such as was done in the radii of activity analysis, one is better able to observe changes in movement patterns associated with breeding females than with movement data calculated between two or three trapping periods (2-4 weeks). Reproductive trends might be lost in these longer time spans where a female could be caring for young one period and the next time trapped be non-pregnant and non-lactating (young weaned).

Plot differences were influenced to a large degree by the *Cavia* in Crovetto Pasture. However, it was notable to observe the smaller radii of activity for *A. azarae* in Plot I compared to those in Hill Plot during the first summer. This is assuming that density was not a critical factor.

Sexual differences in movement lengths and home ranges of small rodents, regardless of species, is the general rule (Blair, 1953; Brown, 1962; Stickle, 1968), with males having somewhat longer movements than females. This is the case here with *A. azarae*, but no definite trend was clearly evident with the other two species.

Whereas most studies demonstrate that rodents have smaller home ranges in the winter than in the summer (Blair, 1953; Stickle, 1968), Hill Plot *A. azarae* appeared to increase their radii of activity during the winter season. By shifting their activity towards the warmer daylight hours, cold temperatures are less of a critical factor, and further movements may result in response to a decreased supply of available invertebrates, seeds, and other foodstuffs. Unfortunately, little movement data are available on southern United States grass-eaters where temperature may be less of a limiting factor than food. Abundant food and/or cover results in smaller ranges than when these resources are limited (Blair, 1953; Stickle, 1968).

Home ranges and movements of mammals are affected by their trophic status (McNab, 1963; Sanderson, 1966). Within the rodents, the insect-eating *Onychomys* have the largest home range and daily movements, followed by the seed-eating *Peromyscus*, (even the insectivorous short-tailed shrew, *Blarina brevicauda* according to Blair (1953), has a range as large or larger than *Peromyscus* captured under similar conditions) and lastly, the grass-eating microtines. The Argentine species studied here showed the same trends. The insectivorous *O. rutilans* were found to have movements longer or at least similar to the seed-eating *O. nigripes*, and *A. azarae*, like the microtines, was active over much shorter distances.

Dispersing and Homing

Dispersal of animals was suggested by Lidicker (1962) to offer three possible advantages to the individual. These are: (1) the disperser might come into contact with more individuals (perhaps also in a more habitable location) and breed more often; (2) the geographic spreading of genetic material increases the chances of new advantageous recombinations of genetic material such that offspring will have greater heterozygosity and increased fitness; and (3) individuals which leave high population densities may in some cases have a higher survivalbility than those which remained during the population crash.

As Myers and Krebs (1971) demonstrated in field populations of *Microtus pennsylvanicus* and *M. ochrogaster*, there appears to be genetic differences between dispersing and resident populations. This supports Howard's (1960) hypothesis that a genetic polymorphism influences the tendency to disperse, and Errington's (1956) and Lidicker's (1962) theory that emigration is a key component of population regulation. Chitty's (1960) hypothesis that a behavioral polymorphism regulates population density was supported when dispersing and resident mice displayed different behavioral traits; A. azarae was examined to approximate losses, by sex and season, from Plot I attributable to dispersal, and not particularly to estimate its value in population regulation.

Sex ratios of A. azarae dispersing into the removal plots show that Crovetto Pasture adults were more likely to retain a 1:1 sex ratio during the winter (non-breeding season). During the second summer (breeding season), the number of females captured dropped significantly. Unfortunately, the removal plots were not in operation the first summer and the low sample sizes of Plot I dispersers discourage meaningful evaluation.

It was noted earlier in the discussion of recruit-resident sex ratios that adult resident female A. azarae typically made up a larger proportion of the sex ratio during the breeding season. It is believed that the opposite trend of fewer female dispersers at this time is due in part to many of the residents becoming established in a set area during the reproductive season. The small number of juveniles is indicative of the fact that A. azarae, like other mice, generally do not disperse until puberty (Blair, 1953; Christian, 1970, Myers and Krebs, 1971).

Myers and Krebs (1971) reported a general excess of dispersing male Microtus in their studies, particularly as their data suggest, during a period of rather intense breeding. Instead of mentioning the above possibility, that is, the sedentary nature of the reproductive females, they believed that the excess of males most likely reflects the fact that males move greater distances, certainly a factor but perhaps not a major one.

Approximately three quarters of the marked A. azarae dispersed no farther than 100 m into the removal plots, based on the four-day monthly trapping tallies. It is assumed that most of the dispersers had become established on the removal plots, and that further dispersal would not continue. The homing data collected for A. azarae indicate that this is true a large proportion of the time. What effect the removal plots had in creating a "sink" which might encourage dispersers to stop moving is a valid point. Dispersal distances given by Blair (1953) for various small mammals and by Stickel (1968) for Peromyscus suggest no great deviation from that observed. A more valid test would be to examine the Activity Plot data and compare the number and distances traveled for Plot I dispersers there with those in the removal plots.

The monthly rate of dispersal appeared to fluctuate some according to severe weather conditions and seasonal (winter) deterioration of the habitat. Concurring with the study by Myers and Krebs (1971) on Microtus, the dispersal rate of A. azarae was found to be rather constant, irrespective of density. However, it may be under seasonal (reproductive?) influences, based on the earlier discussion of dispersal into (recruitment) Plot I.

Homing ability of A. azarae appears to be well developed. The adaptive significance of homing in mice was discussed by Furrer (1973) in his study of homing in Peromyscus maniculatus. According to his work and that by Robinson and Falls (1965) for Microtus pennsylvanicus, the rather constant success at homing in A. azarae might be expected for even greater distances. Where Robinson and Falls found an almost linear relationship in *Microtus* between distance and homing success, Furrer reported a curvilinear function which was formed if long distances (500 m or more) were involved. Whether differences were due to the different social organization and lower mobility of *Microtus* compared to the seed-eating *Peromyscus* is an interesting point considered by Furrer. If in fact further studies substantiate this difference, it would be interesting to find where *A. azarae* fits into the scheme. Unfortunately, the distances examined in this study were rather short.

Activity and Food Habits

Akodon azarae is active day and night, with generally higher peaks of activity during the twilight and the early evening hours. On the other hand, the seed-eating *Oryzomys nigripes* appears to be strictly nocturnal and the insectivorous *Oxymycteris rutilans*, diurnal (pers. data from Activity Plot). A further discussion of their activity patterns and their significance follows.

Activity

Fornes and Massoia (1965) found *A. azarae* to be active day and night during snap-trapping studies in August (winter) at Miramar, Buenos Aires Province, Argentina. Crespo (1966), snap-trapping during various months in the Partido of Rojas, Buenos Aires Province, stated that *A. azarae* was most active during nocturnal hours, while a partially sympatric species, *A. obscurus*, was mainly diurnal. Barlow (1969) likewise discovered the same results with his Uruguayan *A. azarae* and *A. obscurus* snap-trapped during December-May (mainly summer).

In the present study, *A. azarae* became inactive during most of the day and more active during the twilight and evening hours of summer. This trend reversed itself during the winter when evening activity decreased and diurnal activity increased. Presumeably, a shift in activity patterns, in order to avoid temperature extremes, would result in thermoregulatory energy savings for the species. The behavioral flexibility to change activity patterns according to certain climatic factors no doubt accounts for some of the divergence in findings, as does the various methods used in determining the periods of activity.

Oryzomys nigripes were found by Fornes and Massoia (1965) to be nocturnal, although some were captured during the hours of dusk. In addition, they found all but two (out of fifteen) *Oxymycteris rutilans* active between noon and 3:00 pm. Barlow (1969) gave no data for *Oryzomys nigripes*, but found that *Oxymycteris rufus* (= *O. rutilans*) was primarily diurnal although specimens had been trapped at dusk and the early evening. The slightly larger swamp rat, *Scapteromys tumidus*, a less specialized insectivorous mouse (based on stomach morphology) and inhabiting mesic areas in Uruguay with *O. rutilans*, was mainly nocturnal, and thus competition was thought to be minimal.

It appears that all North American grass-eaters (*Microtus*, *Sigmodon*, *Oryzomys*) are generally active both day and night with possible crepuscular peaks (Ambrose, 1973; Baker, 1969; Calhoun, 1945a,b; Hamilton, 1946; Hatfield, 1940; Heidt, 1971; Osterberg, 1962; Pearson, 1959, 1960). *Oryzomys* may be the most nocturnal of the group (Harris, 1953; Negus *et al.*, 1961), but seemingly is the most insectivorous (Sharp, 1967). Seed-eaters (*Peromyscus*, *Reithrodontomys*, and the heteromyids) and insect-eaters (*Onychomys*) are mainly nocturnal (Falls, 1968; Jahoda, 1970; Pearson, 1959, 1960, Reynolds, 1960; Tinkle and Harmon, 1970). With the exception of the insectivorous and diurnal *O. rutilans*, the Argentine species follow the above activity patterns.

Activity patterns and eating habits

Seed- and insect-eaters consume food which is higher in digestible protein and, as Carleton (1973) believed, carbohydrates. Such foods remain longer in the digestive tract. As Kostelecka-Myrcha and Myrcha (1964) demonstrated, even microtines which are fed seeds show a 2.5 to 3 times slower food passage through the alimentary tract than when fed green plant parts. Stomach morphology and food habits of cricetines are rather difficult to correlate completely (Carleton, 1973), mainly because the variety of foods eaten over various seasons is unknown. Studies by Jameson (1952) and Whitaker (1966) on *Peromyscus* and *Mus*, and Batzli and Pitelka (1971) on *Microtus californicus* showed the diversity of foods which may be consumed by a "seed-eater" or a "grass-eater". It is important to point out, however, that grass-eaters eat more seeds than seed-eaters eat of grass. Seed-eaters in turn eat more invertebrate material than most grass-eaters. In this regard, the true status of *A. azarae* remains questionable. Its food habits (author, cursory examination of collected alcoholics; Barlow, 1969) show that animal material may be an important component of its diet at least during some seasons of the year. According to Ellerman (1941), *Akodon* dentition, other than being somewhat hypsodont, unlike oryzomine stock, shows no more modification for grass-eating than related *Calomys*, *Zygodontomys*, or even sometimes *Phyllotis*, possibly the most herbivorous of the group (Dorst, 1971, 1972).

As for *O. nigripes*, Barlow (1969) found that each of ten stomachs examined contained green plant material, while five contained some invertebrate remains. *Oxymycteris rutilans* stomachs (twelve) contained nearly all invertebrate material. The stomachs of the true insect-eaters

(*Onychomys*, *Oxymycteris*, *Scapteromys*) are modified for their specialized diet (Horner, 1962; Horner *et al.*, 1964; Barlow, 1969).

While the activity of grass-eaters is more or less dictated by food requirements that necessitate numerous feeding forays, granivorous and insectivorous species can contain their activity rhythms within a favorable part of the day. For those in the warmer climes, evening presents the time when temperatures are lowest and water, in the form of dew, is most available. Even the grass-eating *Microtus californicus*, which switches to a mainstay of grass seeds during the dry summer months (Batzli and Pitelka, 1971), also assumes a predominately nocturnal activity pattern (Pearson, 1960). Meserve (1971) discovered that *M. ochrogaster* in western Kansas became active mainly during the twilight hours of summer and spring, but diurnal during winter. Through analysis of their droppings, it appeared that the winter mice relied on their underground cached food, and perhaps appeared above ground only when temperatures were less extreme (daylight hours).

In addition to cooler temperatures and more favorable moisture conditions, two other factors may be of importance in influencing nocturnal activity. The first, food availability, is of most importance to insectivorous xeric-inhabiting species such as *Onychomys* where the prey are most active (scorpions) or most easily captured (grasshoppers) during the evening (Horner *et al.*, 1964). To a mesic-inhabiting species (*e.g.*, *O. rutilans*) or even the shrews (Osterberg, 1962), nocturnality evidently is not necessary.

The remaining factor is predation. Pastoral species of canids, felids, mustelids, the hawks, falcons and even some owls that subsist heavily on rodents are commonly diurnal or crepuscular in hunting habits; these are the hours when the largest biomass of rodents, the grass-eaters, are active. It is hypothesized that the nocturnal seed-eaters, because of their active food searching forays through and over plants, would be best protected from predation during the evening. Even when discovered, escape would seem more likely, due to lessened visibility by the predator (since it is evening). These mice also have more of a three-dimensional escape ploy (vertically through the habitat as well as horizontally) compared to the two-dimensional escape pattern (usually along a well established runway system) utilized by grass-eaters. In addition, the fact that seed-eating mice are elusive and less common than their grass-eating coinhabitants would lead to hunting selection away from, not towards, the temporal and spatial requirements of these mice.

A number of pastoral rodent predators are (or at least until recently) inhabitants of the Balcarce area: one fox, two cats, two mustelids, three owls, three hawks or falcons and several snakes. Their potential for effecting selective pressures on the temporal (and spatial) patterns of their prey is probably substantial. However, few if any studies have been conducted which attempt to correlate the temporal hunting strategy of these predators with their prey. Of interest in this vein is the survival value of maintaining a diurnal activity pattern as found in both the insectivorous _O. rutilans_ (does its distinctive smell protect it from predation?) and the similar-sized insectivorous didelphid, _Monodelphis dimidiata_ (pers. data; Fornes and Massoia, 1965).

Several other studies have attempted to compare the dynamics of grass-eaters with seed-eaters, Hansson (1971) presented a comparison of the activity patterns, feeding habits and population dynamics of herbivorous and granivorous mice in Scandinavia. He maintained there was a clear inverse relation between seed and animal food occurrences in granivores which varied according to their needs. The herbivores needed more water than the granivores, probably other or greater amounts of micro-nutrients, and had a more even diel rhythm of food intake than the nocturnal granivores. The need for seed food was very evident in the granivorous species, indicating to Hansson by its effects on the population dynamics of these animals, that there was a causal relationship between fructification and dynamics. Smith (1971), like Hansson, found food to be a limiting factor in the density of *Peromyscus polionotus*, a seed-eater. The primary consumers, like *Microtus*, have failed to show any population increase when food was added under field conditions (Krebs and DeLong, 1965). Smith (1971) then cited a paper by Slobodkin *et al.* (1967) as supporting evidence for the above findings. The latter contended that animals which are plant product consumers or omnivores (*Peromyscus*, *O. nigripes*) are food-limited while those which are vegetation consumers (microtines, probably *A. azarae*) are not.

Eating habits and metabolic rates

Grass-eating myomorphs, like hoofed animals, spend a large portion of their time eating. Grass, unlike seeds or insects, is high in cellulose and low in protein; that is, the mice consume a relatively bulky, low energy food (Elliott, 1963). A rather efficient digestive tract has developed (Golley, 1960) to readily utilize the energy from this type of foodstuff. As a result of a fast passage time of low quality food through the gut (Jameson, 1947), these mice often remain active at various levels over a 24 hour day.

Correlated with their frequent bouts of activity, Hatfield (1939) determined the metabolic rate of *Microtus californicus* to be substantially higher than that for the seed-eating *Peromyscus maniculatus*. He attributed this to the greater feeding activity and likewise with the type of food eaten by *Microtus pennsylvanicus*. Since then, a number of other people, including Packard (1968), have examined other species of microtines and found the same results. Packard believed that a higher rate of metabolism is correlated with the maximal level of heat production that the temperate-derived voles are able to attain during periods of cold exposure.

The grass-eating cricetine *Sigmodon*, Central American in origin, does not show the high metabolic rates of microtines. Bowers (1971) examined several species and geographical races of *Sigmodon*, and found that their resting metabolism was in the range expected for animals of their size. Observations by Cockrum (1948) and Dunaway and Kaye (1961) substantiate the claim that *Sigmodon* reaching their northern limits (Kansas, Tennessee) of North America are not well-adapted for these northern climes. They noted a high mortality during severe winters, and at the least, cotton rats appeared to commonly suffer winter weight losses (Chipman, 1966; Dunaway and Kaye, 1961, 1964; Fleharty *et al*., 1972; Goertz, 1965; Sealander and Walker, 1955). It is known that estimated metabolic needs for *S. hispidus* in Georgia during the winter are nearly 70 percent higher than summer rates (Wagner, 1970). *Oryzomys palustris* may also lose a significant amount of weight from cold stress (Negus *et al*., 1961).

Whether *A. azarae* will be found to be most related in metabolism to that typified by the microtines or the North American grass-eating cricetines (*Sigmodon*, *Oryzomys*) remains to be answered. Some species of *Akodon* are adapted to the much cooler environs of Tierra del Fuego

(Ellerman, 1941), and the altiplano (Cabrera, 1961). Data presented for *A. azarae* by Underhill (1973) on a protein efficiency study suggest that at least some *Akodon* may have a high rate of metabolism. However, the nervousness of *A. azarae* throughout the experiment may have played a role in its slow growth. Experiments presently underway suggest that resting metabolic rates for *A. azarae* are nearly comparable to those of microtines. In fact, following the cytogenetic work of Bianchi *et al.* (1971), the finding of high metabolic rates in this group would support their hypothesis that the akodonts must have radiated from the central Andean region. This region is temperate in nature and would allow *Akodon*, through its metabolic adaptions, to become established where possible in similar areas throughout non-tropical South America. Unlike *Sigmodon* and *Oryzomys*, preliminary examination shows little change in weight (in fact, some gain) in winter *A. azarae*. Similarly, microtine growth data (Krebs, 1964; Krebs *et al.*, 1969) agree with this. In addition, there was very little trap mortality during the colder months. This is in contrast to the seed-eating *O. nigripes* which frequently suffered high winter mortality despite safeguards (boards and cloths over all traps, and cotton or toilet paper inside). This species appeared torpid in the traps a number of times, a phenomenon known to be relatively common in such North American seed-eating cricetines as *Baiomys*, *Perognathus*, *Peromyscus*, and *Reithrodontomys* (Hudson, 1973). It is also known that *O. nigripes* may practice winter huddling. Crespo (1966) excavated several groups consisting of one or more females and young of the year. However, winter huddling, like nest building, food caching, and other activities are found spordically occurring in both grass- and seed-eaters (Dunaway and Kaye, 1961; Frank, 1957; Hart, 1971; Jameson, 1947), and are mechanisms

short of hibernation that provide ways of conserving energy during periods of inactivity and inclement weather. There was not any mortality or torpidity discerned in winter live-trapped O. rutilans.

Runway-making and burrowing activities

Runway-making and burrowing activities, although not limited to grass-eating myomorphs (Baker, 1969, 1971; Hamilton, 1946; Harris, 1953; Jameson, 1947; Stark, 1963; Stickel and Stickel, 1949), are certainly of importance in their biology. Runway-making appears to be of two types. The first is best characterized by most microtines. Their runways are actively maintained by cutting grass and forbs which grow on its surface. These pathways may be short, lasting only a meter or two from the nesting site, or they may extend many meters and interconnect with each other. Sigmodon generally do not seem to produce the complexity or numbers of runways seen in many of the microtines, and Oryzomys palustris may construct even fewer.

The second type of runway-making (made by A. azarae) is found in many of the North American grassland-inhabiting sciurids, such as Spermophilus tridecemlineatus, S. franklinii, and S. beecheyi, the guinea pigs, Cavia and Galea, and some Sigmodon. These animals make runways, generally short (several meters at best), and unless used very frequently, are rather diffuse. Pathways are maintained entirely by constant treading over the vegetation. My observations and those of Barlow's (1969) support the conclusion that neither O. nigripes nor O. rutilans are runway-makers.

Burrowing is another feature well developed in most microtines. These burrows may be extended 15 cm or more into the soil and extend several meters or more in length, with blind tunnels, food storage and latrine compartments, and nesting sites. Sigmodon seem to prefer burrowing into such places as banks, ditches, and under flat rocks or other surface debris. Whatever the case, the burrows are not complex. Oryzomys palustris, due to its generally palustrine habitat, apparently does little digging.

Akodon azarae burrows were only discovered, then examined closely several times. Burrowing does not seem to occupy much of their time, since few were observed. In one case, a hole went straight down for 12-15 cm and ended in a globular nest. In another case, a burrow went 5-10 cm in depth and more or less straight for 30-40 cm in length before it resurfaced. A third burrow was more extensive. One entrance was near a thistle (Cirsium) and the burrow extended down to a depth of 5-6 cm, then leveled off. After a distance of 5-10 cm, a blind tunnel, perhaps under construction, extended 5-10 cm. The main burrow continued onward for 30-40 cm where it ended in a 10-12 cm globular nest. All these burrows were assumed to be those of A. azarae. None, including nests, could be attributed to O. nigripes or O. rutilans. The latter, contrary to its common name of burrowing mouse, did not appear to construct many, if any, burrows, since none was discovered in this study. Instead it is believed that their long foreclaws and shrew-like pointed nose function in digging and rooting for shallow sub-surface invertebrates.

Since little is known of the feeding behavior of the Argentine species, it is pertinent to end this section with several comments on O. nigripes. During the activity study, one individual was viewed by flashlight as it climbed to a height of 1.0-1.5 m to forage on the inflorescences of Paspalum elongatum. Balance was maintained by the relatively large hind feet and long tail, leaving the forefeet free for manipulative tasks. On several other occasions, after trap release during the day, animals, driven presumably by hunger, would immediately climb one of the nearest P. elongatum clumps with amazing agility and commence feeding as described.

To summarize this section, myomorph grass-eaters, including *A. azarae*, are generally active day and night. Species which consume primarily seeds and/or animal material (*Peromyscus*, *Reithrodontomys*, *Oryzomys nigripes*) are mainly nocturnal. When grass-eaters, such as *Microtus californicus* or *Oryzomys palustris* consume a large percentage of seed or animal material, they tend to be more nocturnal. Insectivorous myomorphs (*Scapteromys*, *Onychomys*) and shrews (*Blarina brevicauda*) are mainly active at night or during the twilight hours. A striking exception is the insectivorous *O. rutilans* which is diurnal in its habits.

Alimentary and general metabolic adaptions for consuming a given food type (grass, seeds, insects) in temperate grassland regions and perhaps predation pressure influence to a large degree the basic activity pattern for each group. Food is believed to be a more important factor limiting population density in *O. rutilans* and *O. nigripes* than in the grass-eating *A. azarae*.

Runway- and burrow-making seem to be best developed in temperate grass-eating species. Runways maintained by the animals actively cutting grass and forbs (versus those maintained by trampling) are the most advanced types in grass-eaters. Those with the more tropical, palustrine, or nongrass-eating habits are less advanced burrowers.

Oryzomys nigripes was found to be highly adapted for climbing grasses and forbs in order to consume the still attached seeds. *Oxymycteris rutilans*, like *O. nigripes* did not appear to construct burrows or runways. It is believed that its the long foreclaws and shrew-like pointed nose of the former function in rooting for subsurface invertebrates.

SUMMARY AND CONCLUSIONS

A seventeen-month field study of the comparative ecology and population dynamics of three abundant grassland myomorphs was conducted on several one-hectare sites in the vicinity of Balcarce, Province of Buenos Aires, Argentina. These three species, namely, the herbivorous *Akodon azarae*, the granivorous *Oryzomys nigripes*, and the insectivorous *Oxymycteris rutilans* were compared with their "ecological equivalents", inhabiting temperate grasslands in North America. It was found that:

1. Populations of *A. azarae* during periods of high density exceeded 200 animals/hectare, comparable in density and rate of increase to that found in North American grass-eaters. By late winter the density was reduced to approximately 50 animals/hectare. Although sporadic population irruptions like those of North American *Sigmodon* and possibly *Oryzomys* occur, cyclic population fluctuations like those of microtines have not been reported. Typical of granivores, *O. nigripes* reached 50 animals/hectare the first summer and fall when the seed crop was abundant. By the following winter and early summer, the density was so reduced that several three-day trapping periods would go by before there were further captures. *Oxymycteris rutilans* had the lowest but most stable populations, with densities fluctuating between 3-15 mice/hectare.
2. Sex ratios of *A. azarae* suggested that, like in many other grass-eaters, females make up a higher proportion of the total catch than males during the breeding (summer) season than in the non-breeding season. This was particularly true in resident versus recruit animals.

Oryzomys nigripes consistently had a much smaller proportion of females, a feature common to the social organization of other seed-eaters. The proportion of female O. rutilans was higher, perhaps a function of its continual reproductive activity. Ratios of A. azarae coming into one of the study plots indicated that adult females dispersed less often than males during the breeding season, and about equally during the winter (non-breeding) season.

3. Reproduction of A. azarae, unlike other grass-eaters, from similar latitudes, was strongly seasonal, with litters born from the months of November to April. Litter size averaged 4.6, and gestation length, 22.7 days. Delayed implantation may occur. Young were successfully weaned at 14-15 days of age. The growth rate of the young did not attain the level found in the North American grass-eating microtines. Sexual maturity occurred at two months of age. Young born late in the year did not become sexually mature until the following breeding season. Oryzomys nigripes were noted to breed from January to May. Litter size averaged 3.6, but gestation period was not established. Young were successfully weaned at 14-15 days of age. Sexual maturity may not be reached until the following reproductive season. Oxymycteris rutilans bred in all seasons of the year. Litter size averaged 3.1, but gestation period was not established. Young were successfully weaned at 14 days of age. Sexual maturity occurred near three months of age. Although A. azarae is a seasonal breeder, the species realizes a much higher reproductive potential than the seed-eating O. nigripes or the insect-eating O. rutilans. This agrees well with our knowledge of myomorph grass-, seed-, and invertebrate-eaters in North America.

4. The minimum survival rates for *A. azarae* averaged slightly higher during the winter (80-83 percent) than the summer (59-79.5 percent). Attrition during the winter season indicated that the survival rate was closer to 93-95 percent per fourteen days. *Oryzomys nigripes* had minimum survival rates near 60 percent for the time when they were most abundant. *O. rutilans* was calculated to have a survival rate of 70-76 percent during the summers, but in the winters it was closer to 92 percent. Dispersal, especially in summer, seemed to be a prime factor in lowering the minimum survival rates. Predation appeared to be insignificant. These findings make it difficult to establish whether *A. azarae*, *O. nigripes*, and *O. rutilans* have survival rates comparable to their North American ecological equivalents.
5. The spatial distribution (center of activity) of the mice on the study plots was influenced by vegetative cover. A shift in distribution for *A. azarae* and *O. nigripes* was noted in one plot when increasing numbers of guinea pigs (*Cavia aperea*) caused a deterioration in habitat quality. *Oryzomys nigripes* was captured rather homogeneously, but by the height of the habitat deterioration had disappeared. On another plot where the vegetation consisted of a greater number of dominant grasses, *A. azarae* and *O. rutilans* were generally captured in the most heterogeneous habitat, whereas *O. nigripes* was found in the portion where vegetative cover was most dense and highest.
6. Movements (radii of activity) of *A. azarae* typified graminivorous rodents, being the least of the three species. Winter and male movements were only slightly longer than summer and female movements, respectively. Female movements during a summer of high reproductive intensity were greatly restricted when compared to a summer when

breeding was less intense. The vegetative destruction by *Cavia* seemed to be a factor favoring the increase in the radius of activity of *A. azarae* as the study progressed. Limited data for *O. nigripes* and *O. rutilans* showed only that their movements were 2-4 times more extensive than that for *A. azarae* and in general agreement with their North American counterparts. Dispersal information for *A. azarae* indicated that nearly 75 percent of the mice moved 100 m or less from their previous center of activity. This species homed readily considering the short distances tested (less than 200 m).

7. The diel activity patterns of *A. azarae* and *O. nigripes*, but not the insectivorous *O. rutilans*, agree with what is known of ecologically-similar species in North America. Specifically, the grass-eating *A. azarae* was active at nearly all times, with peaks during the crepuscular hours. The seed-eating *O. nigripes* was active exclusively at night. Unlike the nocturnal insectivorous North American grasshopper mice (*Onychomys*) which inhabit arid grasslands or the mesic-inhabiting shrew *Blarina brevicauda*, *O. rutilans* appeared to be exclusively diurnal. Energy demands and the type of food (grasses, grains, or insects) play a major role in dictating the activity pattern for each species. Although *A. azarae* is the primary myomorph herbivore, it appears to consume more invertebrates than North American grass-eaters. High metabolic rates for *A. azarae* are comparable to those of microtines. Burrowing and runway-making behaviors were less developed in *A. azarae* than the microtines.

The above features indicate that the grass-eating *A. azarae* resembles the North American grass-eating myomorphs in many respects. *Oryzomys nigripes*, in as much as the data will allow, typifies a long-tailed scansorial seed-eater, such as North American grassland forms of *Peromyscus* or *Reithrodontomys*. Only the insectivorous *O. rutilans* is a form not truly represented in North America and appears to have an ecological position overlapping those of both grasshopper mice, *Onychomys*, and shrews such as *Blarina*. The number of grass-eating and seed-eating myomorph species is comparable to that found at similar latitudes in tall grass areas of North America. A total of two myomorph grass-eaters (one uncommon), five seed-eaters (includes *Mus musculus*) and one insect-eater inhabited the study sites. The number of principal myomorph grass-eating species (one) to seed-eaters (four to five) agrees with the hypothesis suggesting that seed-eaters divide their consumer niche more efficiently than the grass-eaters. The seed-eaters of North American grasslands, unlike those found in this study, are augmented slightly in species numbers by the presence of the zapodids (jumping mice) and heteromyids (kangaroo rats, pocket mice). The insectivore niche may also allow several species to inhabit one area. *Oxymycteris rutilans*, and the marsupials, *Monodelphis dimidiata* and possibly *Lutreolina crassicaudata*, appear to fill the insectivore niche normally filled by *Onychomys* and shrews in North America.

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APPENDIX A

APPENDIX A

COMPARATIVE POSTNATAL DEVELOPMENT OF AKODON AZARAE, ORYZOMYS NIGRIPES, AND OXYMYCTERIS RUTILANS

INTRODUCTION

Purpose

This appendix presents the results and discussion concerning the laboratory aspects of a comparative postnatal development study of the three most numerous grassland myomorphs encountered in the field sites, namely, Akodon azarae, Oryzomys nigripes, and Oxymycteris rutilans. These data are then compared with those presently known about their North American grassland counterparts in an effort to determine whether similar adaptional reproductive responses have occurred through the process of convergent evolution.

REPRODUCTION - LABORATORY RESULTS

Postnatal Development of *Akodon azarae*

Methods

Females in advanced pregnancy were separated from the harem (1♂ to 3-5♀♀) and maintained in separate cages. When the gestation length was being established, the male was also transferred to take advantage of the postpartum estrus. Litter checks were made at least once per day and often twice until the young were born. When found, the litter size and sex were noted and each neonate was measured, in mm, for total, tail, hind feet, and ear lengths, and also weighed to the nearest 0.1 g. These measurements, taken while the animal was etherized, were thereafter taken at weekly intervals to the twelfth week, by which time the animals continued to gain only an imperceptible amount. During this period various other developmental characteristics, such as hair growth, incisor eruption, hearing, eye opening, sexual maturation, and molting patterns were noted.

Most long-term growth measurements were taken from 19 litters. Sample sizes varied from one age to another due to cannibalism (common for certain females within the first few days postpartum), death (accidental or after new harems were established), tail loss, pregnancy, or failure to measure. All animals were maintained on a commercial mouse chow and an *ad libitum* water supply.

Gestation period

In most cases, male *Akodon* remained with the female during pregnancy and for some 24 hours after partuition, if separated from her at all. Based on vaginal smears for sperm, there is a postpartum estrus of undetermined length. However, the little available data indicated that if the female was not inseminated within 24 hours of parturition, she would not be receptive again for several days. From this procedure, an estimate of gestation length was made. Of eleven females on which the time of insemination was known, gestation length ranged from 20-25 days, with a mean of 22.7 days. A female nursing six young during pregnancy had the longest gestation period, 25 days, but another female nursing three had the shortest, 20 days.

Litter size

Of 43 A. azarae litters raised in the laboratory, there was a mean of 4.6 young per litter, a mode of 4, and a range of 2-10. This average litter size was not significantly different ($p>.05$) than that found for Plot I and Hill Plot animals (4.3, mode 4, range 1-8, N=120) palpated for young, although the variance was higher ($p<.05$) in the lab colony. There were neither differences ($p>.05$) in mean litter size between the two breeding seasons of Plot I nor between the second breeding seasons (Hill Plot was established after the first season) of Hill Plot and Plot I.

Although females outnumbered males by a ratio of 1.2:1.0 in the laboratory stock, a goodness of fit X^2 test showed no significant difference at the .05 level from the expected 1:1 sex ratio. A negative correlation between litter size and neonate weight was found (N=22, $r=.60$, $p<.01$). Data in Table I-A show this correlation at both extremes of litter size, and also the range of variation in weights within litters. By examining field records, it was possible to find the approximate weight

Table A-1. Relationship of litter size to mean weight, and weight variation within, compared to between litters in *Akodon azarae*.

Litter size	Mean Weight	Range	Litter size	Mean Weight	Range
2	3.25	3.0-3.5	6	2.40	2.1-2.8
2	3.15	3.1-3.2	6	2.25	1.9-2.4
2	2.70	2.6-2.8	6	2.70	2.3-3.1
3	3.03	2.6-3.3	6	2.27	2.1-2.4
3	2.70	2.6-2.9	7	2.71	2.2-2.6
3	2.57	2.5-2.7	7	2.41	2.2-2.6

Table A-2. Frequency distribution at age when the developmental characteristics of incisor eruption, hearing, and eye opening first appeared in *Akodon azarae*.

	LOWER INCISORS			UPPER INCISORS				HEARING					EYE OPENING					
	At least one incisor erupted							First Observed					At least one eye fully opened					
DAY	5	6	7	5	6	7	8	7	8	9	10	11	10	11	12	13	14	15
No. Indiv.	1	12	8	1	8	9	3	15	29	20	2	1	6	15	45	14	2	1
Percent	4.8	57.1	38.1	4.8	38.1	42.9	14.3	19.7	53.3	29.9	3.0	1.5	7.2	18.1	54.2	16.9	2.4	1.2
Mean Day	6.3			6.7				8.2					11.9					

of a female when she was known not to be pregnant, as determined by palpation. An attempt was made to correlate this weight with the number of palpable embryos found within her one trapping period earlier or later. At times several periods in either direction were examined if the animal was mature and her weight appeared stable. The results, both plots pooled, demonstrate that there is a positive correlation ($N=110$, $r=.21$, $p<.05$) between palpable litter size and female weight.

Physical development

Within the first 24 hours (Figure A-1) the neonate's dorsum, including the head, tail, top of the feet, and plantar tubercles, were slightly pigmented. Only the eyelids were darkly pigmented. Laterally, the dorsal pigmentation blended into the venter and the flesh-colored remaining portions of the body. Conspicious through the venter skin were the incompletely fused sternal elements and the superficial aspects of the milk-filled stomach, the intestine, and liver.

The eye lens were not generally visible because of the very pigmented eyelids. Portions of the frontal and parietal cranial sutures were evident through the skin. The ears, their peripheral edges slightly pigmented, were not folded at birth. Although unpigmented, the claws were well-developed, but extended only slightly beyond the ungual phlanges. A few white hairs were generally scattered over the head and the dorsum and appeared to be the future guard hairs. These hairs, especially those on the head, were visible with the naked eye, but were best observed with stereo-binocularscope. The white mystacial vibrissae were well-developed, the longest reaching approximately 3 mm in length.

The neonate was generally not vocal when handled. There was no ability to upright itself. The tail was normally found tucked between the legs for the first few days. Many young, aside from the typical uncoordinated movements, were capable of performing a springing action. This movement, started from the normal, slightly doubled position of the resting neonate, resulted in a very quick straightening of the body and a kicking outwards. At times, litter mates would likewise respond, resulting in a major disturbance. This type of behaviorism has also been noted in Reithrodontomys humulis (Layne 1959).

At approximately 4 days of age, (Figure A-2) the neonate was able to right itself, although any quick crawling movement was likely to send the animal sprawling. The dorsal guard hairs, more plentiful by now, were approximately 1 mm in length. The yellowish-tipped underfur, barely above the skin surface, was present at this age or day 5 on the head and possibly neck region, and in a few of the more advanced neonates, the anterior portion of the back. The onset of underfur growth gave the mouse a velvet-textured coat during this stage. There was usually a substantial amount of epidermal scaling in a wide area in front of the advancing underfur. The venter was coated with a sparse covering of white guard hairs about 0.5 mm in length. The sternal elements had fused and the visceral organs noted earlier were slightly less visible because of a thicker, more pigmented skin.

By the age of 7 days (Figure A-3) almost all A. azarae had the dorsal underfur present over the entire dorsum while in the remaining, the underfur was lagging very slightly on the rump area. The guard hairs were approaching 2.0 mm in length, while the underfur was approximately 0.5-0.1 mm. Underfur on the ears, legs, and feet was well-developed. Epidermal scaling continued laterally and also occurred on the upper hind limbs. Scaling began on the pectoral region, and in some, on the lower

Figure A-1. Neonate *Akodon azarae*.

Figure A-2. Four-day-old *Akodon azarae*.

Figure A-1

Figure A-2

Figure A-3. Seven-day-old *Akodon azarae*.

Figure A-4. Fourteen-day-old *Akodon azarae*.

Figure A-3

Figure A-4

portions of the venter where underfur appeared. In most cases, the underfur was less than 0.5 mm in length, the guard hairs, 1.0 mm. The liver and stomach were still fairly conspicious through the venter skin. The nipple areas were just slightly distinguishable from the surrounding skin. The longest mystacial vibrissae were 8-10 mm. Little behavioral change had occurred since previously. The mice were more steady on their feet than at four days, but still had problems maintaining their balance. At least some continued to kick abruptly when disturbed, but others, especially later, were beginning to crawl out of the nest, scurrying aimlessly.

At 14 days of age (Figure A-4), A. azarae was well-developed (see next paragraph also), and many could be weaned. The dorsal underfur was approximately 5.0-7.0 mm, while the guard hairs were 8.0-9.0 mm in length. The ventral underfur was about 3.0-4.0 mm, and the guard hairs 5.0-6.0 mm in length, thus hiding all signs of the viscera and nipple areas previously described. The longest mystacial vibrissae measured about 11.0-12.0 mm. The incisors, white-tipped for the first 0.5-1.0 mm after eruption, still showed some white, although this area would disappear within the next week or two.

From the fifth day and terminating at weaning, another series of rather important developmental characteristics also appeared. Table 2-A gives the days at which incisor eruption, hearing, and eye opening were first observed in A. azarae. The young Akodon were tested for response to sound by holding the mouse within several inches of the mouth, then producing a loud sound with the tongue and roof of the mouth. Such a stimulus invariably elicited a startle response from those animals which had developed hearing.

Although weaning of animals under laboratory conditions was highly artificial, data for *A. azarae* indicated that under conditions of available food and water, the mice could be weaned within 1-3 days after eye opening; that is, at approximately two weeks of age.

Molt

Barlow (1969) discussed molt patterns of Uruguayan *A. azarae*, based on field-trapped animals. Consequently, no detailed study of molt patterns was undertaken here. However, during weekly postnatal measurements of animals, certain features were noted. A post-juvenile molt was observed on the venter of 35-day-old animals. Several animals sacrificed at 21 days showed no evidence of melanin deposition on the skin, while it was very evident on the venter of 28-day-old individuals. Apparently this post-juvenile molt, difficult to observe in live animals (only on venter here) because of the similarities in hair color and texture between juveniles and adults, lasted for several weeks. Some animals first noticed with a venter molt pattern at 35 days continued to show pelage changes until 63 days of age.

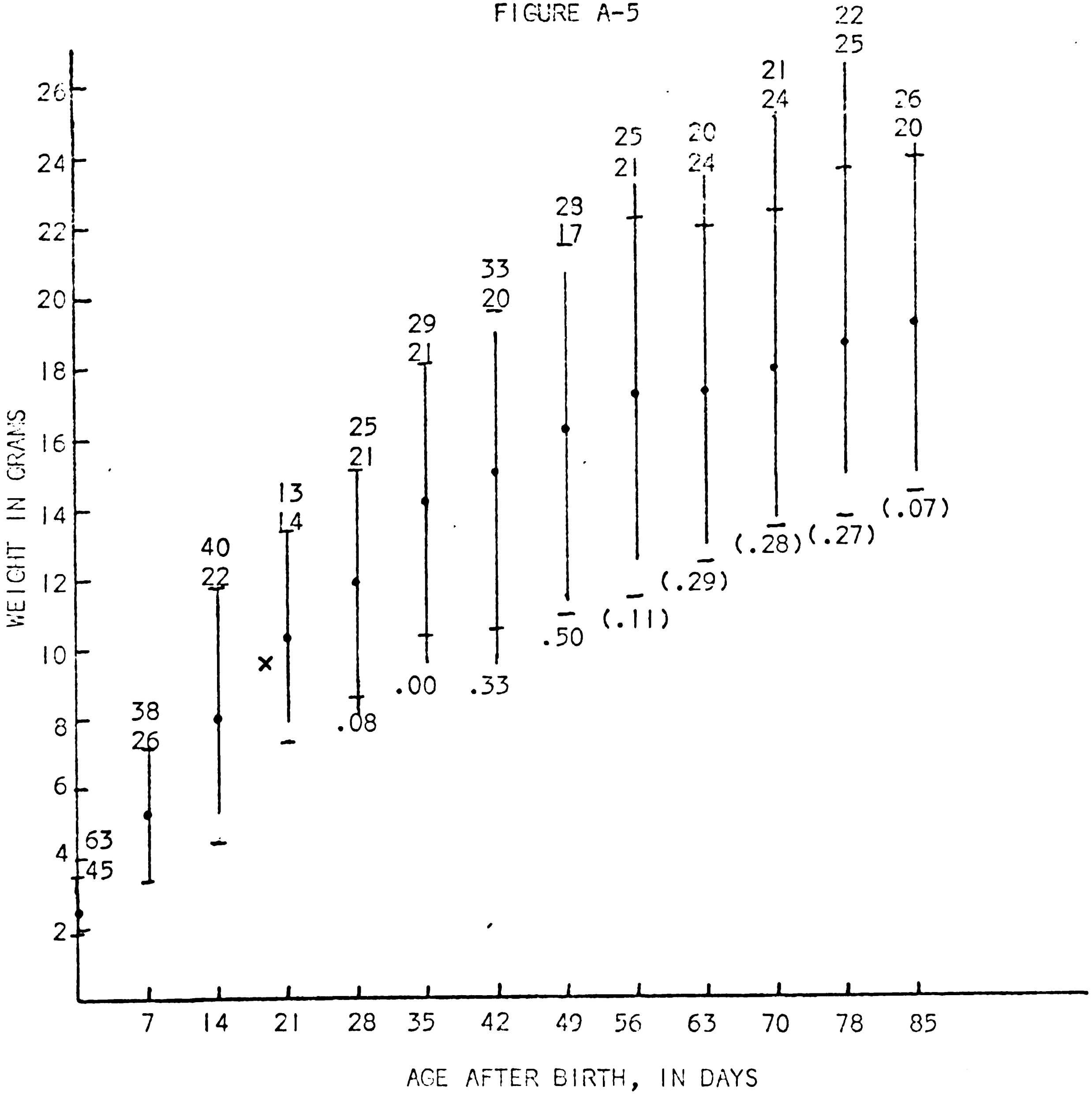
Growth- weight gain and maturation

The mean weight of 108 neonate *A. azarae*, pooled sexes, was approximately 2.5 g, about 13 percent of the adult female weight, based on the average for 84-day-old laboratory-raised individuals. If based on field data, females averaging approximately 25 g produced young. On this basis, the neonate is about 10 percent of the female weight. In terms of average adult weight, the mean *A. azarae* neonate litter weight, based on the mean litter size of 4.6 as determined in the lab, was 60.5 percent, or about 45 percent if weights of field data animals are considered.

The growth by weight of neonate *Akodon* to maturity, with the mean,

Figure A-5. Mean weight, range, and ± 2 SE for pooled sexes of *Akodon azarae*. Numbers above the mean designate female (top) and male (bottom) sample sizes. Numbers below the mean without parentheses give the proportion of perforate females to total females; those with parentheses give the proportion of pregnant females to total non-nursing females.

FIGURE A-5


WEIGHT IN GRAMS
26
24
22
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16
14
12
10
8
6
4
2
AGE AFTER BIRTH, IN DAYS
7
14
21
28
35
42
49
56
63
70
78
85
63
45
38
26
40
22
13
14
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.08
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21
.00
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20
.33
28
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21
(.11)
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21
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(.27)
26
20
(.07)
×

± 2 S.E., range, and sample sizes, is shown in Figure A-5. Proportional growth, mean, and range of weight measurements are shown for each seven day period from birth to 84 days of age in Table A-3. Growth continued beyond 84 days of age (12 weeks) but only at a very slow rate. Approximate time of one-halt growth was also calculated.

Laboratory reared 84-day-old young appeared to weigh the same as similar-sized individuals snap-trapped in the field. To test this, head-body lengths of 84-day-old lab born mice were divided into 5.0 mm increments. Then the body lengths, similarily apportioned, of the same approximate number of snap-trapped mice were taken from field data for the summer period, January-February 1969. The mean weights within each body length increment did not differ significantly ($p > .05$). Sexes were pooled since there was no significant difference between the means. However, there was a strong tendency in later weeks for adult males to weigh more, than adult females. This tendency was significant ($p < .05$) in most of the winter (non-reproductive) populations from both field plots where mean weights were compared.

Aging by weight alone is not accurate because each age group exhibits considerable variation (Figure A-5). Even so, weight quickly separates live-trapped animals into rather crude age categories. Individual _A. azarae_ were considered to be juveniles if equal to or less than 12 g in weight, at which time they were approximately 30 days of age. Since weaning occurred when the mice were approximately 14 days of age, they were a part of the trappable population for about two weeks. Subadults were those animals weighing more than 12 g but less than 18 g, a mean weight they approached at about 60 days of age.

By this age, the first female _Akodon_ showed signs of pregnancy by palpation (embryo detection was not possible until after the first 7-10 days). From that point in time, pregnancies continued at a moderate rate (Figure A-5). Male maturation, based on scrotal development and manual phallic protrusion, appeared in several animals (4.7 percent) at about 35 days of age. By the age of 60 days (male mean weight, 17.3 g), all the males were sexually well-developed although this was not the case in the field. For the purpose of this study, adults, regardless of sex, were considered to be those animals that weighed 18 or more grams.

Out of approximately a dozen harems where the males were as old or older than the females, the first litter was not born until the males were: 83, 91, 98, 99, 100 days old. Since the gestation period for *A. azarae* is approximately 23 days, the youngest male did not breed until about 60 days of age. Perhaps experienced, mature females mated to young males would give a better indication of male sexual maturity (but experience indicated that older animals do not readily accept introductions).

Geometric growth rate

Geometric growth rates provide a sensitive basis of comparison of growth patterns. The mean instantaneous rate of growth was calculated from the change over time in mean weight of a number of animals.

Brody (1945) gives the formula for instantaneous rates of growth as $K=\frac{\log W2-\log W1}{t2-t1}$, or more simply, $k=\log \frac{W2}{W1} t$, where k=instantaneous relative rate of growth for a given unit of time, $\frac{W2}{W1}$=ratio weight at t2 to weight at t1, and, t=time interval in days between observations.

Figure A-6 shows the mean weight of *Akodon*, sexes combined, plotted on a semi-log scale for the first 84 days (12 weeks). The slope of the line, representing the instantaneous rate of growth, approximates a

Figure A-6. Weekly average rate of growth (weight) for pooled sexes of *Akodon azarae*. The straight lines roughly indicate the instantaneous rate of growth. Sample sizes are given above each point.

FIGURE A-6

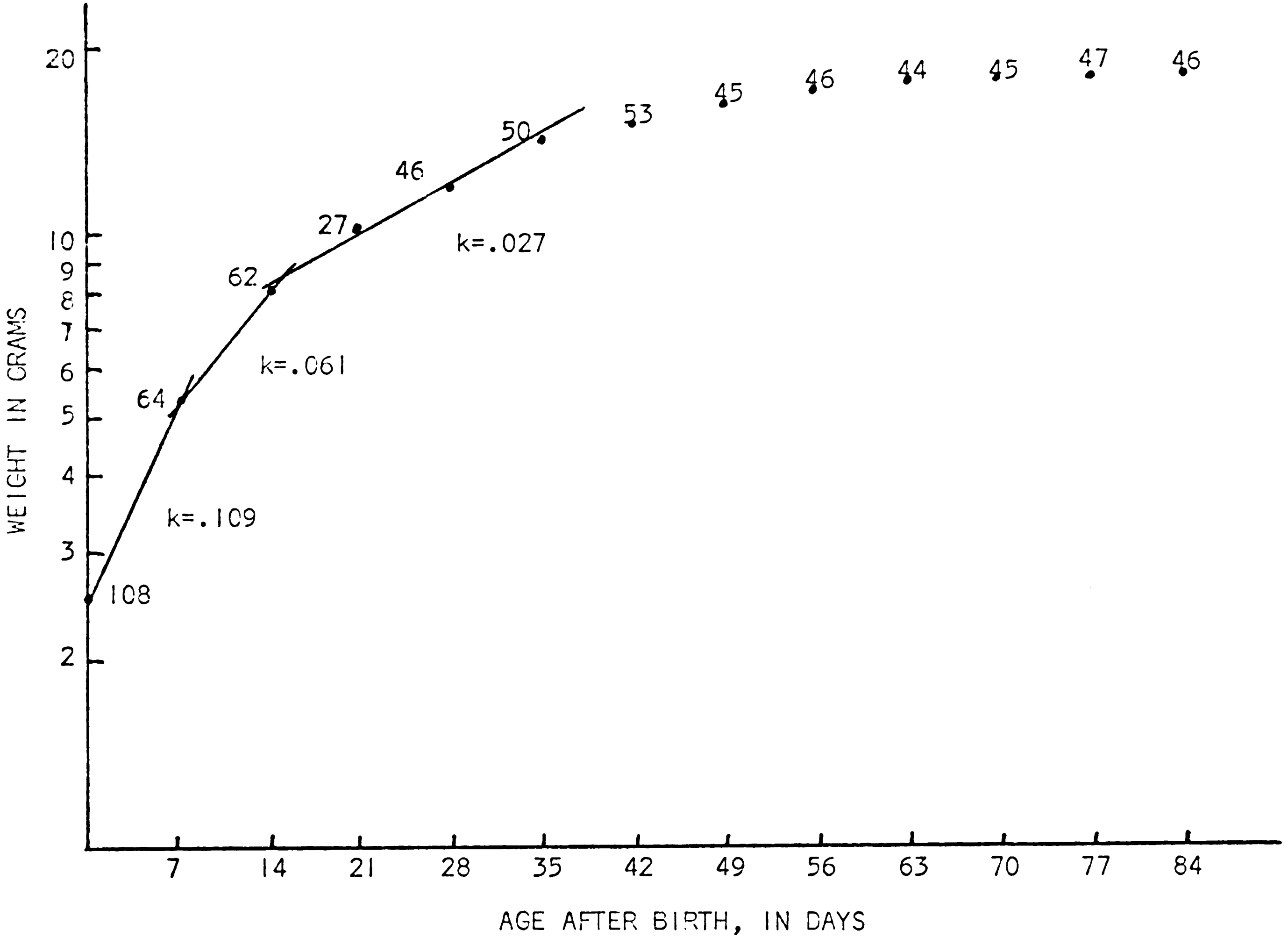
20
10
9
8
7
6
5
4
3
2
WEIGHT IN GRAMS
108
64
62
27
46
50
53
45
46
44
45
47
46
k=.109
k=.061
k=.027
7
14
21
28
35
42
49
56
63
70
77
84
AGE AFTER BIRTH, IN DAYS

Table A-3. Proportional growth (in percent), means, ranges, daily instantaneous rate of growth (I.R.G.), and approximate age at one-half growth for total, tail, body, hind foot, and ear lengths, and weight for *A. azarae*. All calculations based on 84-day-old adult measurements.

	AGE IN DAYS						
	Day of Birth	7	14	21	28	35	42
TOTAL LENGTH							
Prop. growth	33.5	49.8	68.1	78.7	82.5	87.9	91.6
Mean	(55.2)	(81.9)	(111.9)	(129.4)	(135.6)	(144.6)	(150.7)
Range	49-60	72-91	96-130	121-146	120-154	135-160	138-164
I.R.G.	---	.056	.045	.020	.008	.009	.006
TAIL LENGTH							
Prop. growth	20.5	39.1	65.3	76.6	83.5	89.6	93.4
Mean	(13.9)	(26.4)	(44.1)	(51.7)	(56.5)	(60.6)	(63.1)
Range	11-17	24-33	37-53	43-56	49-68	53-70	57-72
I.R.G.	---	.092	.073	.023	.012	.010	.006
BODY LENGTH							
Prop. growth	42.6	57.3	70.1	80.2	81.7	86.3	89.8
Mean	(41.3)	(55.6)	(68.0)	(77.8)	(79.3)	(83.7)	(87.2)
Range	36-46	46-61	59-77	72-85	71-86	74-91	79-92
I.R.G.	---	.042	.029	.019	.003	.008	.006
HIND FOOT							
Prop. growth	38.5	63.6	84.0	90.6	94.2	96.2	98.0
Mean	(7.7)	(12.6)	(16.7)	(18.0)	(18.7)	(19.1)	(19.5)
Range	7-8	11-15	15-19	16-20	17-21	18-21	18-21
I.R.G.	---	.071	.040	.011	.005	.003	.003
EAR LENGTH							
Prop. growth	21.3	43.6	77.1	86.8	92.8	95.6	97.5
Mean	(3.0)	(6.0)	(10.7)	(12.0)	(12.8)	(13.2)	(13.5)
Range	2-3	5-8	8-13	10-15	12-14	13-15	12-15
I.R.G.	---	.102	.082	.016	.009	.004	.003
WEIGHT							
Prop. growth	12.9	27.6	42.3	54.0	62.0	74.1	78.5
Mean	(2.5)	(5.3)	(8.2)	(10.4)	(12.0)	(14.3)	(15.1)
Range	1.9-3.2	3.4-7.5	5.4-13.0	7.9-13.8	8.2-15.1	9.6-18.5	11.0-20.0
I.R.G.	---	.109	.061	.033	.022	.024	.008

Table A-3 (Continued).

	AGE IN DAYS						
	49	56	63	70	77	84	1/2 growth (days)
TOTAL LENGTH							
Prop. growth	94.6	96.7	98.3	99.3	99.7	100.0	
Mean	(155.6)	(159.0)	(161.7)	(163.2)	(163.9)	(164.4)	7.1
Range	140-167	145-170	147-172	149-174	150-175	153-175	
I.R.G.	.005	.003	.003	.001	.001	.000	
TAIL LENGTH							
Prop. growth	96.1	97.8	99.4	99.6	99.6	100.0	
Mean	(64.9)	(66.1)	(67.2)	(67.3)	(67.3)	(67.6)	9.9
Range	58-72	58-74	61-74	62-74	62-73	61-72	
I.R.G.	.004	.003	.002	.000	.000	.001	
BODY LENGTH							
Prop. growth	93.4	95.5	96.9	97.9	98.6	100.0	
Mean	(90.6)	(92.7)	(93.8)	(94.9)	(95.7)	(97.0)	3.5
Range	81-99	83-100	83-101	86-103	88-104	90-105	
I.R.G.	.005	.003	.002	.002	.001	.002	
HIND FOOT							
Prop. growth	98.5	99.0	99.7	99.4	99.9	100.0	
Mean	(19.6)	(19.7)	(19.8)	(19.8)	(19.9)	(19.9)	3.2
Range	17-21	17-21	18-21	18-21	18-21	18-21	
I.R.G.	.001	.001	.001	.000	.001	---	
EAR LENGTH							
Prop. growth	97.5	98.0	99.2	99.7	101.2	100.0	
Mean	(13.5)	(13.6)	(13.7)	(13.8)	(14.0)	(13.8)	8.3
Range	13-14	13-15	13-15	13-15	13-15	13-15	
I.R.G.	.000	.001	.001	.001	.002	---	
WEIGHT							
Prop. growth	84.5	89.6	90.0	93.4	92.8	100.0	
Mean	(16.3)	(17.3)	(17.3)	(18.0)	(17.9)	(19.3)	18.6
Range	11.4-21.5	12.5-23.3	12.9-23.5	13.7-29.7	14.9-26.6	14.9-25.7	
I.R.G.	.011	.009	.000	.006	.000	.010	

straight line for short distances. The rates of growth based upon the trend of the average weight growth curves have been calculated for the first week at k=.109, and for the second, k=.061. For the growth of Akodon from birth to day 7, the value of k=.109 signifies that the instantaneous percentage rate of growth is approximately 10.9 percent per day during that 7 days of growth. Table A-3, in part, gives instantaneous rates of growth of weight by 7 day time increments.

Growth - body measurements

Proportional growth (percentage of total, based on that of 84-day-old adults), mean values, ranges, and instantaneous rates of growth for *A. azarae* are given in Table A-3 for measurements of total lengths of tail, head and body, hind foot, and height of ear from notch for weeks 0-12. The head-body and hind foot lengths of the neonate, when compared to those of the adult, were disproportionally longer than other body measurements, while the tail and ear were much shorter. However, the tail and ear grew faster during the first 14 days, thus reducing this difference. The approximate age of one-half growth, also shown in Table A-3, is a reliable index of postnatal development, and like proportional growth or growth rate measurements, is often used when comparing different populations or taxa.

Postnatal Development of *Oryzomys nigripes*

Methods

The data presented here are limited; two pair of adults gave birth to four litters and because of cannibalism, escape or sickness, only two animals survived past 84 days. Weights measurements, and observations were made as in *A. azarae* unless noted differently. Animals were maintained on a diet of mixed grain (oats, wheat, cracked corn, sorghum) and an *ad libitum* water supply.

Litter size and gestation period.

Of three litters observed shortly after birth, all contained four young. Field data (Table 14) show the litter size to average 3.6. One female gave birth 44 days after her previous partituation, although the gestation period was certainly shorter than this. One field animal was captured in alternating trapping periods, and in each instance was in advanced pregnancy. This indicates a gestation period nearer 28 days.

Growth and maturation.

At birth, the neonate weighed 2 g (to the nearest gram), about 11 percent and the litter, approximately 44 percent the weight of a 18 g adult (field data). Standard measurements and weight of *O. nigripes* are given only for the first 21 days and again at 84 days (Table A-4). The mean instantaneous rate of growth, also included in the above table was calculated for the first 21 days; the percentage of total growth, based on the measurements of the two 84-day-old individuals are also shown.

Individual *O. nigripes* were considered to be juveniles if equal to or less than 7 g in weight, at which time they were about 30 days old. Those more than 7 g but less than 11 g were classified as subadults, or approximately 30-90 days of age. Individuals weighing 11 or more grams were designated as adults. The adult age class was established somewhat more arbitrarily than that for *Akodon azarae*. None of the lab animals showed any external signs (e.g. perforate vagina, scrotal testes) of sexual maturity during the 84 day postnatal development study. However, field data (Table 18) suggest that some animals near the 84 day weight were becoming sexually mature.

Table A-4. Proportional growth (in percent), means, ranges, daily instantaneous rate of growth (I.R.G.) and approximate age at one-half growth for total, tail, body, hind foot, and ear lengths, and weight for *Orvzomys nigripes* and *Oxymycteris rutilans*. All calculations based on 84-day-old adult measurements.

	Oryzomys nigripes AGE IN DAYS					
	Day of Birth	7	14	24	84	1/2 growth (days)
TOTAL LENGTH						
Prop. growth	31.5	47.1	64.6	77.6	100.0	
Mean	54.7	81.8	112.1	134.6	173.5	8.1
Range	53-56	77-86	108-115	126-140	173-174	
I.R.G.	---	.057	.045	.027	---	
TAIL LENGTH						
Prop. growth	18.4	38.6	58.6	76.8	100.0	
Mean	17.7	37.1	56.3	73.7	96.0	11.0
Range	16-19	35-38	50-61	70-77	96.0	
I.R.G.	---	.106	.060	.038	---	
BODY LENGTH						
Prop. growth	47.7	57.5	72.1	78.6	100.0	
Mean	37.0	44.6	55.9	60.9	77.5	1.6
Range	36-38	42-48	54-61	56-63	77-78	
I.R.G.	---	.027	.032	.012	---	
HIND FOOT						
Prop. growth	31.3	54.8	75.2	84.3	100.0	
Mean	7.2	12.6	17.3	19.4	23.0	5.6
Range	7-8	12-14	16-18	19-20	23.0	
I.R.G.	---	.080	.045	.016	---	
EAR LENGTH						
Prop. growth	16.0	32.0	72.8	85.6	100.0	
Mean	2.0	4.0	9.1	10.7	12.5	10.1
Range	2.0	4.0	8-11	10-12	12-13	
I.R.G.	---	.099	.117	.023	---	
WEIGHT						
Prop. growth	19.0	33.3	38.1	57.1	100.0	
Mean	2.0	3.5	4.0	6.0	10.5	18.3
Range	2.0	3-4	4.0	5-7	10-11	
I.R.G.	---	.079	.027	.058	---	

Table A-4 (Continued).

Oxymycteris rutilans

	AGE IN DAYS					
	Day of Birth	7	14	21	84	1/2 growth (days)
TOTAL LENGTH						
Prop. growth	---*	---	---	---	---	
Mean	74.2	109.0	146	---	---	---
Range	70-80	109.0	146	---	---	
I.R.G.	---	.055	.042	---	---	
TAIL LENGTH						
Prop. growth	---*	---	---	---	---	
Mean	19.6	31.0	45.0	---	---	---
Range	17-23	31.0	45.0	---	---	
I.R.G.	---	.065	.053	---	---	
BODY LENGTH						
Prop. growth	42.3	60.5	78.3	81.4	100.0	
Mean	54.6	78.0	101.0	105.0	129.0	2.7
Range	51-57	78.0	101.0	105.0	129.0	
I.R.G.	---	.051	.037	.006	---	
HIND FOOT						
Prop. growth	40.0	65.4	80.8	88.5	100.0	
Mean	10.4	17.0	21.0	23.0	26.0	2.8
Range	9-12	17.0	21.0	23.0	26.0	
I.R.G.	---	.070	.030	.013	---	
EAR LENGTH						
Prop. growth	26.9	56.3	75.0	87.5	100.0	
Mean	4.3	9.0	12.0	14.0	16.0	5.5
Range	4-5	9.0	12.0	14.0	16.0	
I.R.G.	---	.106	.022	.019	---	
WEIGHT						
Prop. growth	12.5	22.9	39.6	54.2	100.0	
Mean	6.2	11.0	19.0	26.0	48.0	19.0
Range	5-8	11	19	26	48	
I.R.G.	---	.082	.078	.045	---	

*Tail incomplete in 84-day-old animal, so no proportionate measurements possible.

Physical development

The *O. nigripes* neonate (Figure A-7) was pigmented lightly above; this pigmentation faded laterally into the flesh-colored venter. The eyelids were the darkest pigmented part of the individual although the lens remained visible. The ankles and tail dorsum were slightly pigmented, as could be the plantar tubercles. The cranial sutures were visible as were the rib cage, liver, and milk-filled stomach. The ears were folded at birth but parted within the first 24 hours. The white mystacial vibrissae were approximately 3 mm in length. Hair, if present, was barely visible over the dorsum and head regions. The neonates at times emitted high pitched squeaks of several seconds duration when disturbed. No other conspicious behavioral features were observed.

At four days of age (Figure A-8), the dorsal guard hairs were approximately 1 mm in length. Brownish underfur, visible for the first time, covered most of the head and dorsum, with the exception of the rump area. Conspicious at its leading edges was the epidermal scaling, most evident on the sides of the dorsum, around the ears, and the upper parts of the limbs. Sparse guard hairs, approximately 0.5 mm in length were visible on the venter for the first time. The rib cage, liver, and stomach remained visible. The young were readily able to upright themselves from a smooth surface by this time. Crawling too was well-developed.

By 7 days of age (Figure A-9) the dorsal guard hairs were 2-3 mm in length, the underfur about 1 mm. Ventrally, the guard hairs were 1-2 mm, the underfur, 1 mm or less in length. Some epidermal scaling was occurring on the venter. The liver and stomach were still visible through the ventral hair. The nipples of the female were easily distinguishable. The longest mystacial vibrissae approached 7 mm in length. Out of a litter of four

Figure A-7. Neonate *Oryzomys nigripes*. Note folded ears.

Figure A-8. Four-day-old *Oryzomys nigripes*.

Figure A-7

Figure A-8

Figure A-9. Seven-day-old *Oryzomys nigripes*.

Figure A-10. Fourteen-day-old *Oryzomys nigripes*.

Figure A-9

Figure A-10

animals, all could hear for the first time and had their eyes open at least a slit. The lower incisors were near eruption, the uppers less so. The young balanced extremely well and remained motionless or crawled on one's finger without falling. The tail was actively utilized for stabilization.

At fourteen days (Figure A-10) the young, probably weaned by now, were well-furred, very active, but still somewhat clumsy in their movements, a condition not observed by 21 days.

Postnatal Development of *Oxymycteris rutilans*

Methods

As with *O. nigripes*, the data here also are limited. More than 12 pregnant females live-trapped in areas outside of the study grids, then brought into the lab, lost their young through abortion, reabsorption, or cannibalism. One female successfully raised one of four young (she ate one, and two others were lost in a fostering experiment with the coney rat, *Reithrodon auritus*). Attempts to breed *Oxymycteris* in the lab failed. Animals were maintained on a diet of mixed grain, like that given to *O. nigripes*, and meat (mice or *Cavia* flesh) several times per week, and an *ad libitum* water supply.

Litter size and gestation period

Of the three litters observed shortly after birth, all contained four young. Field data (Table 15) show the litter size to average 3.1. At birth, the neonate weighed 5-8 g (average, 6.2 g), about 12.5 percent, and the litter, approximately 52 percent of the weight of a 48 g adult. If based on field data, females averaging 86 g produced young. On this basis, the neonate is about 7, and the litter, 22 percent of the female weight. Several field animals were captured in alternate trapping periods, and in a few instances were in advanced stages of pregnancy. This suggests a gestation period near 28 days.

Growth and maturation

Standard measurements and weight for O. rutilans are given only for the first 21 days and again at 84 days (Table A-4). The instantaneous rate of growth, also included in the above table was calculated for the first 21 days; the percentage of total growth, is based on the measurements of the one 84-day-old individual.

Individual O. rutilans were considered to be juveniles if equal to or less than 28 g in weight, at which time they were about 30 days old. Those more than 28 g but less than 48 g were classified as subadults, or those approximately 1-3 months of age. Individuals weighing 48 g or more were designated as adults. Like in Oryzomys nigripes, the adult age class was established somewhat arbitrarily. None of the lab animals showed any signs of sexual maturity during the 84 day post-natal development study. However, field data (Table 18) suggest that some animals near the 84 day weight were becoming sexually mature.

Physical development

The O. rutilans neonate (Figure A-11) was lightly pigmented above but faded laterally into the flesh-colored venter. The eyelids were the darkest pigmented part of the individual, although the lens remained visible. The ankles, dorsal aspects of the feet, tail, dorsum, and the plantar tubercles were pigmented. The cranial sutures were visible as was the rib cage, liver, and stomach. The ears were not folded at birth. The white mystacial vibrissae were approximately 5 mm in length. The dorsum and head were sparsely covered with erupting guard hairs.

Like the former two species, the young were not observed to remain attached to the nipples of the female when she left the well-constructed nest. The young at times emitted 2 or 3 squeaks of short duration when handled. No other conspicious behaviorisms were observed.

By four days of age (Figure A-12), the entire head and dorsal areas were covered with a dense but short (under 1 mm) coat of light rusty-colored underfur; the guard hairs were approximately 2 mm in length. Epidermal scaling occurred at the leading edges of the pelage, particularly on the lateral surfaces and on the hind legs. Little development was observed on the venter; the sparse guard hairs were approaching 1 mm in length, and the nipple areas were faintly visible. The white-tipped lower incisors were barely erupted; the uppers were present the following day. The young maintained their balance well, but crawling was less developed.

At 7 days of age (Figure A-13), the dorsum was covered with guard hairs 4 mm and underfur 2 mm in length. The venter, with the visceral organs barely visible, was coated with underfur 1.0-1.5 mm, and guard hairs 3 mm in length. The epidermal scaling was essentially completed. The teats were easily observed. The one remaining animal was responsive to sound for the first time, and had both eyes slightly open. When touched or a sharp sound was made, the rodent jerked violently away. Adults often responded similarily when disturbed.

By 14 days of age (Figure A-14), the young were well-furred and adult-like, and probably acquired most of their own food. Barlow (1969) identified the rather strong odor which emanates from this species as reminiscent of acrolein (acrylic aldehyde). This chemical is used commercially to warn of toxic odourless gas leaks from mechanical systems. Barlow hypothesized that this strong, penetrating scent may serve to discourage potential predators.

Figure A-11. Neonate Oxymycteris rutilans. Note the darkened plantar tubercles.

Figure A-12. Four-day-old Oxymycteris rutilans.

Figure A-11

Figure A-12

Figure A-13. Seven-day-old *Oxymycteris rutilans*.

Figure A-14. Fourteen-day-old *Oxymycteris rutilans*.

Figure A-13

Figure A-14

DISCUSSION

The laboratory postnatal development data given for Akodon azarae, Oryzomys nigripes, and Oxymycteris rutilans were not presented merely for the reason that little was known of their postpartum ontogeny. It was anticipated that sufficient information would result which could lead to an understanding of what reproductive attributes are shared by these three species with their ecological equivalents in the temperate grasslands of North America. For a more thorough discussion of the evolution of South American myomorphs and the role of natural selection in effecting changes dealing with reproduction and postnatal development for a given species within a specific habitat and consumer level, one is also advised to read the DISCUSSION found in the main text.

Gestation Period

Gestation period (Table A-5) is the first reproductive parameter examined which shows some very definite trends. Almost without exception, the grassland inhabiting and grass-eating microtines are characterized by a gestation period of 20-22 days which is little affected in length (i.e.,no delayed implantation) by other energy demands on the female, mainly the nursing of its current offspring. This is not the case with a few microtines specialized for other niches (the tree mouse, Phenacomys longicaudus, Hamilton, 1962; the woodland inhabiting bank vole, Clethrionomys glareolus, Brambell and Rowlands, 1936), at least some murids (Mus musculus, Daniel, 1910; Rattus norvegicus, King, 1913), and cricetines (most Peromyscus, Layne 1968; Onychomys, Egoscue, 1960;

Table A-5. Gestation period, average neonate and adult weights, average litter size, percent of neonate and litter weight to that of the adult for some grassland inhabiting North American and Argentine grass-, seed-, and insect-eating myomorphs.

	Gestation Period (days)	Average Neonate Weight	Average Litter Size	Average Adult Weight	Percent Neonate to Adult Weight	Percent Litter to Adult Weight	Source
Akodon azarae	22.7	2.5	4.6	19-25	10.0-13.2	46.0-60.5	Present study
Microtus oregoni	23-24	1.7	3.0	25	6.8	20.4	Cowan & Arsenault (1954)
M. pennsylvanicus	21	2.7	5.3	45	6.0	31.8	Hamilton (1941)
M. californicus	21-22	2.7	4.8	62	4.4	20.9	Selle (1928)
M. montanus	20.5-21.0	2.2	4.5	40	5.5	24.8	Seidel & Booth (1960)
M. ochrogaster	21	2.8	3.2	44	6.4	20.4	Martin (1956)
Clethrionomys rutilus	---	1.75	6.7	26	6.7	45.1	Morrison *et al.* (1954)
Dicrostonyx rubricatus	21-22	3.1	3.0	50	6.2	18.6	Morrison *et al.* (1954)
Phenacomys ungava	≅21	2.4	4.8	27	8.9	42.7	Foster (1961)
Sigmodon hispidus (La.)	27	6.8	5.6	150	4.5	25.4	Meyer & Meyer (1944)
S. arizonae (Mexico)	---	8.5	6.3	261	3.3	20.5	MSU lab colony
S. fulviventer (Mexico)	---	7.1	4.5	175	4.1	19.3	MSU lab colony
Oryzomys palustris	25	3.1	5.0	55	5.6	22.2	Hamilton (1946); Negus *et al.* (1961); Svihla (1931)
Onychomys leucogaster	26-37	2.8	3.6	30	9.3	33.6	Horner (1968); Pinter (1970)
O. torridus	27	2.4	3-5	20	12.0	48.0	Horner & Taylor (1968); Pinter (1970)
Oxymycteris rutilans	±28	6.2	3.1	86	7.2	22.3	Present study
Oryzomys nigripes	±28	2.0	3.6	18	11.1	40.0	Present study
Reithrodontomys humulis	24	1.2	3.2	8.2	14.6	46.8	Dunaway (1968); Kaye (1961); Layne (1959)
R. megalotis	23-24	1.5	2.6	12.8	11.7	30.5	Cockrum (1952); Smith (1936); Svihla (1931)
*Peromyscus maniculatus**	23-27	1.6	3.05	15	10.7	32.5	Svihla (1932)

*For other species of *Peromyscus*, see Layne (1968).

Svihla, 1936). Grass-eating cricetines such as *Oryzomys palustris* and *Sigmodon* have very precocial young, whose dependence on their mother is less, so delayed implantation as an energy conserver would be of questionable value.

In contrast to the short gestation period of microtines, the seed-eaters (*Reithrodontomys*, *Peromyscus*) have a period slightly longer, with the insectivorous species (*Onychomys*) the longest. It is presumed that the same selective forces are acting on the Argentine species; *A. azarae*, the main myomorph herbivore, has a reasonably short gestation intermediate between that of microtines and the cricetid seed-eaters. Unfortunately, we can only speculate at this date that *O. nigripes*, the seed-eater, and *O. rutilans*, the insect-eater, would have correspondingly longer gestation periods according to their respective consumer level. How true this trend will be for *O. rutilans* is questionable. Its larger size and more mesic affinities, when compared to *Onychomys*, may mask any clear-cut differences. Layne (1968), discussed the importance of these factors in *Peromyscus*.

Postpartum Estrus

According to Conaway (1971), postpartum estrus seems to have developed independently many times and its distribution is sporadic throughout mammals. Asdell (1964) noted that it follows no phylogenetic pattern. As an example, it does occur in many but not all species of *Peromyscus* (although this is a point of contention; see Rood, 1966), the gain or loss of postpartum estrus is one of the most easily made of the major reproductive adjustments. Its main purpose in small short life-span mammals seems to be as a mechanism for increasing productivity. With exception of some *Peromyscus* listed by Asdell and *Oryzomys nigripes* and *Oxymycteris rutilans* on which it was not established, all other species in Table A-5 are known to have a postpartum estrus.

Litter Size

Average litter sizes (Table A-5) show a very definite positive trend towards larger litter sizes with grass-eaters but generally smaller litters for seed- and insect-eaters. The three Argentine species examined here also show this trend.

Reproductive Efficiency

Frank (1957) mentioned that one of the factors which affects the reproductive potential of a species is its reproductive efficiency. This is computed as the average litter size weight divided by the average weight of the reproducing females, times 100 percent. What this measurement strongly suggests is that one species is putting an equal, more, or less of an "investment" into reproduction at a given time compared to another species. Frank found that *Microtus arvalis* litter weight amounted to 53.2 percent of the mother's weight, while in most other small rodents, 20-30 percent is the average (Table A-5; Layne, 1968). Neonates of *Akodon azarae* are relatively large when compared to adult weight, and with the respectable litter size, both contribute to the high reproductive efficiency found in this species. Several dissimilar species in Table A-5 show equally high reproductive efficiencies (e.g., *Reithrodontomys humulis*, *Onychomys torridus*, *Clethrionomys rutilus*).

Growth - Weight

Daily instantaneous rates of growth (Table A-6) for the first week of growth (where greatest differences in rates are found) were calculated for a number of different species to determine if different rates could be found which would parallel their food habits. Layne (1968) calculated growth rates for various species of *Peromyscus* and found a substantial

Table A-6. Daily instantaneous rates of growth for approximately the first week for some grassland inhabiting North American and Argentine grass-, seed-, and insect-eating myomorphs.

Species	Days after birth	k	Source
Akodon azarae	0-7	.109	Present study
A. olivaceus	0-7	.100	MSU lab colony
Microtus oregoni	0-9	.162	Cowan and Arsenault (1954)
M. pennsylvanicus	0-7	.152	Hamilton (1941)
M. californicus	0-7	.168	Hatfield (1935)
M. montanus	0-7	.114	Seidel and Booth (1960)
M. ochrogaster	0-7	.131	Martin (1956)
Clethrionomys rutilus	0-7	.157	Morrison *et al.* (1954)
Dicrostonyx rubricatus	0-7	.149	Morrison *et al.* (1954)
Sigmodon hispidus (Louisiana)	0-10	.108	Meyer and Meyer (1944)
S. fulviventer (Durango)	0-7	.129	MSU lab colony
Oryzomys palustris	0-7	.114	Hamilton (1946)
Oxymycteris rutilans	0-7	.082	Present study
Onychomys leucogaster	0-7	.090	Horner (1968)
O. torridus	0-7	.084	Horner and Taylor (1968)
Oryzomys nigripes	0-7	.079	Present study
Reithrodontomys humulis	0-7	.087	Layne (1959)
*Peromyscus maniculatus**	0-7	.129	Layne (1968)

*For other species of *Peromyscus*, see Layne (1968).

amount of variability at the subspecific as well as specific levels. The data presented here does indicate a generally higher growth rate in the herbivorous microtines. However, the other species listed, including those from Argentina, regardless of food habits, have somewhat lower values.

Physical Development

Not all growth is devoted to increasing the amount of flesh, *per se*. Much of the energy utilized by the young goes into the development of homeothermic (including pelage growth), and locomotor control. Other ontogenetic changes, such as tooth formation, eye opening, hearing and other complex neuromuscular advances also must take place before the young can be weaned. Table A-7 examines the data for the development of incisor eruption, hearing, eye opening, and perhaps the most ill-defined but nevertheless most important development of all, weaning.

Concerning the latter, King *et al*. (1963) attempted to define weaning in deer mice as the age at which the young mice gain weight (lab chow, water, ad libitum) upon separation from the female and litter mates. Whether this definition will withstand the rigors of testing under field conditions remains to be answered. Most results in the literature show weaning to occur from several days to a week after eye opening, depending upon the species and the investigator.

Although there appears to be slight species differences in developmental times, *Sigmodon* is the most precocial (Table A-7) myomorph in North America and possibly the western hemisphere. This genus has a gestation length the same (e.g., *Onychomys*) or only slightly higher than other species listed on Table A-5. This genus is at one extreme where neonate weight is less than what might be expected for a 27-day-old

Table A-7. Time of first observance of several developmental characteristics in some grassland inhabiting North American and Argentine grass-, seed-, and insect-eating myomorphs. Time expressed in days.

	Incisors	Hearing	Eye Opening	Weaning
1-*Akodon azarae*	6-7	8	12	14-15
2-*Microtus pennsylvanicus*	6-7	7-8	8-9	12-14
3-*M. californicus*	4-6	7-8	9-10	14
4-*M. montanus*	5-6	10-12	10	12-15
5-*M. oregoni*	5.5	10	10-11.5	13
6-*M. ochrogaster*	1	8-9	10-11	16
7-*Clethrionomys rutilus*	2	-	9-10	17-18
8-*Sigmodon hispidus* (Louisiana)	1-2	Sev. days	1-2	10-20
9-*S. fulviventer* (Mexico)	0-1	0-2	1-2	10-20
10-*Oryzomys palustris*	5	-	8	11-13
11-*Onychomys leucogaster*	10-11	15	18-20	23
12-*O. torridus*	10-11	14	16-20	20
13-*Oxymycteris rutilans*	5	7	7-8	14
14-*Oryzomys nigripes*	8-9	7?	7-8	14
15-*Reithrodontomys humulis*	6-7	8-9	7-8	21
16-*R. megalotis*	4-5	9	11-12	19-21
17-*Peromyscus maniculatus**	5.2	12-13	12-14	18

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*For other species of *Peromyscus*, see Layne (1968).

1-Present study
2-Hamilton (1941); Godfrey (1953); pers. data
3-Selle (1928); Hatfield (1935); Jenkins Foundation for Research, Salinas, California (pers. comm.)
4-Seidel and Booth (1960)
5-Cowan and Arsenault (1954)
6-Kruckenberg *et al.* (1973); Martin (1956)
7-Morrison *et al.* (1954)
8-Odum (1955); Svihla (1929); MSU lab colony
9-MSU lab colony
10-Hamilton (1946)
11-Horner (1968)
12-Horner and Taylor (1968)
13-Present study
14-Present study
15-Kaye (1961); Layne (1959)
16-Smith (1936); Svihla (1931)
17-Svihla (1932); King (1958); King *et al.* (1963); Huff (1973)

(gestation time) individual in relation to the adult. Reproductive strategy for these large herbivorous cricetines appears to have directed energy not into biomass but instead into features which allow precociality, and hence independence (at relatively small size) from the mother within a very short time. Oryzomys palustris is another species which has a rather precocial development.

Second to the grass-eating Sigmodon and Oryzomys in physical development are most of the microtines. They not only maintain a high growth rate but in addition are capable of independence by two weeks of age. Other North American species (Onychomys, Reithrodontomys, and Peromyscus average another week longer before weaning. The three Argentine species are notable because each was successfully weaned by 14 days of age.

Sexual Maturity

In relatively short-lived species such as that found in most rodents under natural conditions, sexual maturity at an early age would be a obvious asset, and therefore an important attribute of reproductive potential.

Under lab conditions, a few female Akodon azarae have a perforate vagina by four weeks of age, although as a group it is not until they attain 6-8 weeks of age before perforation and the first pregnancies are commonly noted. Males do not seem to start breeding until they too reach two months. Oryzomys nigripes young showed no change from the non-perforate, non-scrotal condition during the 12 weeks in which they were observed. Weights of field animals indicate that 12 weeks is the very earliest at which both sexes even begin to show signs of sexual maturation. Oxymycteris rutilans data also indicate that animals (at least females) are just starting to reach sexual maturity at 84 days of age (twelve weeks). Reproductive maturity for these latter two species then, is delayed two to three times longer than that found for *A. azarae*.

The microtines (Table A-8) are characterized by their extremely early date of sexual maturity. Frank (1957) in particular mentioned a specific example where the European *M. arvalis*, which suckle until the seventeenth day, have shown a perforated vagina by the eleventh and were mated by old males by the thirteenth. Other grass-eaters noted (i.e., *Sigmodon hispidus* and *Oryzomys palustris*) are rather precocial in their development, considering their adult size. Seed-eaters and insect-eaters on the other hand, generally mature no faster than and usually slower than these larger herbivores.

Table A-8. Age of sexual maturity, in weeks, in some grassland inhabiting North American and Argentine grass-, seed-, and insect-eating myomorphs.

Species	Age of Sexual Maturity (in weeks)	Source
Akodon azarae	6-8	Present study
Microtus sp.	4-6	Frank (1957); Hamilton (1941); Martin, (1956); Cowan and Arsenault (1954); Seidel and Booth (1960); Hatfield (1935)
Phenacomys ungava	4-6	Foster (1961)
Sigmodon hispidus	6-7	Meyer and Meyer (1944)
Oryzomys palustris	7	Hamilton (1946)
Oryzomys nigripes	12+	Present study
Onychomys leucogaster	13.5	Svihla (1936)
O. torridus	6-7	Horner and Taylor (1968)
Oxymycteris rutilans	12+	Present study
Reithrodontomys humulis	8-12	Layne (1959)
R. megalotis	13	Svihla (1931)
*Peromyscus maniculatus**	5-7	Layne (1968)

*For other species of *Peromyscus*, see Layne (1968).

SUMMARY

The comparative postnatal development of three Argentine grassland inhabiting myomorphs was presented; namely, *Akodon azarae*, the predominant grass-eater; *Oryzomys nigripes*, a peromyscine-like seed-eater; and the large (86 g) insect-eating *Oxymycteris rutilans*. Results demonstrate that among the three, *A. azarae* most likely has the shortest gestation period, the largest neonate to adult weight ratio, the highest reproductive efficiency, the fastest first week of growth, by weight, a nearly equal or slightly slower development in incisor appearance, attainment of hearing, eye opening, and weaning date, and lastly, a much quicker time of sexual maturity. *Oryzomys nigripes*, in relation to *O. rutilans*, has a higher neonate to adult weight ratio, a higher reproductive efficiency, a slightly slower first week of growth, a slower rate of incisor eruption, but comparable development in hearing, eye opening and day of weaning. Sexual maturity appears to take a lengthy period of time for development in both species; field data suggests that it may take longer in *O. nigripes*. Concerning *O. rutilans* alone, the rather precocial development of this large mouse in the areas of incisor eruption, hearing, eye opening and day of weaning is notable.

In comparison to North American grassland myomorphs, the same basic pattern exists. The grass-eaters, particularly the microtines, have the fastest postnatal development. The microtines are alone in having a very fast growth rate. Even those which have a moderate growth rate (a measure of biomass only) have the available energy transformed into precocial development of locomotion, eye opening, and other physical-behavioral factors. Reproductive efficiency does not seem to be characteristic of microtines. Instead, it commonly appears in the smaller species of many groups, and functions to maintain litter sizes at the level of their larger relatives, all other variables being equal.

The seed- and insect-eating species are more alike in many of their developmental features. This may be attributed to their food habits, which probably overlap more than do the grass-eaters with either one. *Akodon azarae* appears to be intermediate in ontogenetic development to the grass-eaters and seed-eaters. *Oryzomys nigripes* are equally or slightly more precocial than *A. azarae*, but produce smaller litters and reach sexual maturity at a later date, as in seed-eaters. *Oxymycteris rutilans*, other than sharing a similar diet and possibly a delayed sexual maturation, is unlike *Onychomys*, its only myomorph counterpart in North America. *Oxymycteris* is more precocial in its early development, is nearly triple the size of *Onychomys* at adulthood, and reaches sexual maturity at a rather late age, but then commences to breed thorughout the year. The fact that *Onychomys* commonly inhabits xeric areas where selective forces would presumably differ may help in explaining the divergence between the two animals.